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ECOLOGICAL AND BEHAVIORAL IMPACTS OF ARTIFICIAL PRODUCTION STRATEGIES ON THE ABUNDANCE OF WILD SALMON POPULATIONS

A Review of Practices in the Pacific Northwest

By

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SUMMARY

Production hatcheries play a major role in supplying Pacific salmon and trout to the common property fishery, and benefiting commercial, sport, tribal, and non-tribal fishers. In the Pacific Northwest hatchery fish currently contribute between 70-80% of coastal fisheries.

In the past production hatcheries have also played a role in slowing the decline of natural populations. Now, however, they are becoming increasingly implicated as one of the factors causing the decline. Among their citations include the transplantation and straying of fish, over-harvest, and effects on carrying capacity of receiving environments.

Most production hatcheries were built when wild salmon stocks were healthy, and genetic diversity of stocks was not a concern. Today, many stocks in the Pacific Northwest are listed as threatened or endangered under the terms of the U.S. Endangered Species Act (ESA), and the need to preserve biodiversity has brought about a new era of management strategies for the conservation of wild stocks. As current hatchery practices and methods are now recognized as contributors to the overall decline, there have been strong arguments for the reform of hatchery management, particularly in the Columbia River Basin. The goal is to reduce the overall impact of hatchery fish on the survival of wild stocks.

This document reviews the issues behind the major theoretical and observed ecological and behavioral impacts of salmonid hatchery production strategies on the abundance and trends of wild salmonid populations. The major focus is on potential effects of differing artificial production strategies as they relate to stocks within:

- the ESU (evolutionarily significant unit) of spring/summer chinook (*O. tshawytscha*) in the Snake River, and
- the ESU of steelhead (*O. mykiss*) in the Upper Columbia River.

The document is divided into three principal sections, as follows:

Comparison of Hatchery and Wild Salmon Biology

Some major differences between hatchery and wild salmonids are reviewed in sections describing survival, foraging behavior, social behavior, habitat preference, response to predators, differences in morphology and physiology, and reproductive behavior. The reviews conclude that artificial culture environments condition salmonids to respond to food, habitat, conspecifics, and predators differently than fish reared in natural environments. Present culture techniques also alter selection regimes, which may result in genetic divergence between hatchery and wild populations. Finally, the phenotypic differences observed between cultured and wild fish are both genetically and environmentally controlled.

Impacts of Artificial Production Releases on Wild Fish

The impacts of hatchery reared fish on the population abundance of wild fish are reviewed and discussed in five sections concerning the effects of artificial production releases (supplementation) on wild fish population abundance, competitive social interactions, predation, health, and migratory behavior. Each section provides relevant conclusions drawn from the review.

Conclusions and Recommendations

The final section draws some overall conclusions from the completed reviews and analyses, and makes recommendations. It includes summary tables which detail an assessment of the potential effects of artificial production strategies on population abundance of wild spring/summer chinook and steelhead in their respective ESUs. In this section the authors conclude that hatchery strategies offer the potential to stabilize and amplify salmonid populations, but the artificial environment conditions salmonids to respond in ways different from fish reared in natural environments. Fundamental changes in the dynamics of hatchery production policy and implementation may be necessary both where hatchery supplementation is used to maintain some populations until underlying causes of decline are corrected, and where production hatchery operations overlap listed stocks. However, the overall effectiveness of supplementation to maintain a population until underlying causes of decline are corrected is unknown. Little specific numerical information exists regarding population abundance dynamics or interactive factors, therefore assessments can only be prescribed in directional trends rather than absolute values.

Finally, the authors conclude that the direction of future use of artificial propagation in the Columbia Basin will be a function of both the status of the natural populations and their habitats. For supplementation and recovery purposes, the productivity of naturally spawning populations will be a key parameter. Current information is not adequate to assess properly the potential effects of hatchery operations on wild stocks. The authors recommend that the Region should focus research to develop policies and procedures which properly integrate the roles of hatcheries for conservation and sustainability of salmonid populations. Artificial propagation risks may be ameliorated by development and implementation of conservation hatchery protocols which may improve fitness and survival of hatchery fish.

The report includes a bibliography of some 270 citations.

CONTENTS

I. INTRODUCTION

Development of the hatchery system for Pacific salmon (*Oncorhynchus sp*.) began in the late nineteenth century and ever since it has played an increasingly prominent role in enhancement of the resources throughout the Pacific Northwest. Most public hatcheries were built originally to mitigate for loss of natural spawning habitat, and their goal was simply focused on enhancing the harvest of adults in the commercial fisheries. In the Columbia River Basin alone, for example, there are now nearly 100 hatcheries. They produce about 200 million juveniles each year, which provide up to 80% of the fish in several key salmon fisheries. Today, these hatcheries play a major role in supplying salmon and trout to the common property fishery, and benefiting commercial, sport, tribal, and non-tribal fishers. Unfortunately, they are so instrumental in supplying fish that it is nearly impossible to separate the management of the fisheries from the management of the hatcheries.

The majority of production hatcheries were built at a time when wild salmon stocks were healthy, and genetic diversity of stocks was not a concern. However, times have begun to change. With the near catastrophic decline of Pacific salmon species on the west coast of the United States many stocks have been listed as threatened or endangered under the terms of the U.S. Endangered Species Act (see Matthews and Waples 1991, Nehlson et al. 1991, Waples et al. 1991a and 1991b, Hard et al. 1992, Schmitten et al. 1995, and Weitkamp et al. 1995). The need to preserve biodiversity has brought about a new era of salmon fisheries management strategies for the conservation of wild stocks. This unquestionably will have an increasing impact on the operation and management of production hatcheries, and the traditional users of hatchery fish.

The public hatchery system in the Pacific Northwest may have slowed the decline of some natural salmon populations. However, current hatchery practices and methods have been considered significant factors leading to the overall decline of several salmonid species. Recently, the National Research Council (NRC) called for the reform of hatchery management in the Columbia River Basin, including changes in the approach, operation, and expectations from artificial propagation (NRC 1996).

The overall impact of hatchery fish can be divided into three broad categories. First, over-harvest of wild stocks in mixed stock fisheries can have a profound impact on survival of wild stocks. When abundant hatchery stocks are targeted for high harvest, less abundant wild stocks cannot withstand the high exploitation rates, resulting in under-escapement of wild fish. Second, there are a number of detrimental ecological interactions that can take place between hatchery and wild fish. These can take the form of competition for food and territory, predation by larger hatchery fish preying on smaller wild cohorts, and negative social interactions when large numbers of hatchery fish are released on top of small numbers of wild fish. Third, there is a series of genetic risks associated with hatchery rearing. Where hatchery operations conflict with recovery of ESA-listed stocks the options appear to be either, 1) isolation of hatchery production (e.g., near-tidewater rearing/release and terminal harvest), or 2) altering hatchery operations to include a conservation mandate.

This document reviews the issues behind the major theoretical and observed ecological impacts of salmonid hatchery production strategies on the abundance and trends of wild salmonid populations. The effects of genetic manipulations are intrinsically involved in these impacts. Genetic risks (such as hybridization, inbreeding depression, outbreeding depression, etc.) have been discussed extensively in recent publications (Hindar et al. 1991, Waples 1991, Busack and Currens 1995, Campton 1995, Waples 1995, Allendorf and Waples 1996, NRC 1996, Waples 1999).

Genetic risks are not considered in detail in the present document. Rather, the major focus is on potential ecological and behavioral effects of differing artificial production strategies as they relate to stocks within:

- the ESU (evolutionarily significant unit) of spring/summer chinook (*O. tshawytscha*) in the Snake River, and
- the ESU of steelhead (*O. mykiss*) in the Upper Columbia River.

The document is divided into four major sections. Following this brief Introduction, Section II outlines the general differences in morphology, behavior, life history, and survival imposed by artificial production strategies on hatchery fish compared with wild fish. Section III details the effects of artificial production releases (supplementation) on wild fish population abundance, competitive social interactions, predation, health, and migratory behavior. Section IV draws some overall conclusions and makes recommendations. It includes summary tables detailing an assessment of the potential effects of artificial production strategies on population abundance of wild spring/summer chinook and steelhead in their respective ESUs.

II. COMPARISON OF HATCHERY AND WILD SALMON BIOLOGY

Introduction

Salmon culture at Pacific Northwest hatcheries is conducted in a plethora of configurations of rearing vessels running the continuum from earthen ponds through small vats, circular tanks, and large production raceways. All conventional rearing techniques, except perhaps earthen ponds, share the common feature of being geared toward mass-production under conditions which are best described as ‘unnatural’.

Maynard et al. (1995) describe hatchery conditions as, “Groups of fish … reared in the open, over uniform concrete substrates; conditioned to minimal raceway flow regimes; provided no structure in which to seek refuge from water current, predators, or dominant cohorts; held at high, stress-producing densities; surface fed; and conditioned to approach large, moving objects at the surface.” Similarly, Reisenbichler and Rubin (In press) state, “Seemingly the only similarities in hatchery and wild environments for salmonids are water and photoperiod.” It is therefore not surprising that fish reared under these ‘conventional’ regimes are markedly different from their wild counterparts in behavior, morphology, survival, and reproductive ability. Some of the major differences between hatchery and wild salmonids are summarized in Table1, and described in detail in the following pages.

Table 1. Relative differences between wild and hatchery reared salmonids.

Category	Wild	Hatchery
Survival		
egg-smolt survival	lower	higher
smolt-adult survival	higher	lower
Behavior[a]		
foraging ability	efficient	inefficient
aggression	lower	higher
social density	lower	higher
territorial fidelity	higher	lower
migratory behavior	disperse	congregate
habitat preference	bottom	surface
predator response	flee	approach
Morphology		
juvenile shape	more variable	less variable
nuptial coloration	brighter	duller
kype size	larger	smaller
Reproductive potential		
egg size	smaller	larger
egg number	lower	higher
breeding success	higher	lower

[a] Behavioral deficits of hatchery fish tend to remediate over time as hatchery fish acclimate to the post-release environment

Survival

Although the protective nature of hatchery rearing increases egg-to-smolt survival (see overviews of Leitritz and Lewis 1976, Piper et al. 1982, Pennell and Barton 1996, etc.) the post-release survival of cultured salmonids is often considerably lower than that of wild-reared fish. Studies during the 1950s and early 1960s were the first to document that the survival of hatchery-reared fish released in the natural environment is often significantly lower than that of their wild-reared counterparts. Over a period of several years Greene (1952) recovered wild brook trout fingerlings at rates 8.4 to 18.6 times higher than those of hatchery fingerlings planted in the same lake. Salo and Bayliff (1958) found the survival of seaward migrating smolts of wild coho salmon was three times better than that of their hatchery-reared counterparts. Reimers (1963) found that 30% of rainbow trout planted in streams died within 44 days of release, while only one wild trout died during the same period.

In some of these early studies it is not clear if survival differences between hatchery- and wild-reared fish were primarily the result of genetic or environmental differences. The work of Miller (1953) suggests both genetic strain and rearing environment play a role in the post-release survival of hatchery produced fish. He found that only 5% of hatchery-reared cutthroat trout planted in streams survived a year after release, compared with 46% of the transplanted wild trout during the same period. Stream-reared hatchery fish had an intermediate survival value of 17.2%.

Research conducted since the mid-1960s suggests that poor post-release survival of hatchery fish represents both adaptive differences between hatchery and wild populations, and environmental differences between hatchery and natural rearing environments. When Mason et al. (1967) compared survival of wild, domestic, and hybrid strains of brook trout, reared from fertilization to parr under identical environmental conditions, they found that each pure strain was best adapted to its own rearing environment. In their study, wild brook trout showed the poorest growth and survival in the hatchery, but 10.2% survived when released into test stream sections compared with only 3.6% survival for hybrid trout and 0.7% for domestic trout. Apparently the rearing environment also affected post-release survival, as almost twice the number of naturally-reared wild fish (19.7%) survived compared with hatchery-reared wild fish (10.2%) after both were transplanted into test stream sections.

Fraser (1981) stocked equivalent numbers of domestic, wild, and domestic/wild hybrid strains of brook trout in nine lakes. In six of the lakes he recovered wild fish at a rate two to four times above that of domestic fish. In the three other lakes the recovery rate was similar for all three strains. In a subsequent study (Fraser 1989) he concluded that wild and hybrid strains established self- perpetuating breeding populations more frequently than pure domestic strains released into the same lakes.

LaChance and Magnan (1990a, 1990b) found that wild and hybrid strains of brook trout survived in lacustrine habitats better than a domestic strain planted in the lake during the same period. All three strains were reared from eggs in the hatchery before being released into lakes, and were influenced by the presence of intra- and inter-specific competitors.

Poor survival of both hatchery strains in natural environments and wild strains in hatchery environments suggests that selection, in many cases, has resulted in the genetic divergence of hatchery populations from their wild ancestors. Reisenbichler and McIntyre (1977) examined the growth and survival of hatchery, wild, and hatchery-wild hybrid strains of steelhead trout reared from eggs under identical conditions in streams and a hatchery pond. Again, each pure strain was best adapted to its environment, with more wild fish surviving in the stream and more hatchery fish surviving in the hatchery. Hybrid fish surviving in the stream grew faster than their wild counterparts, whereas hatchery fish grew faster in the hatchery pond.

In studies by Chilcote et al. (1986) and Leider et al. (1990), naturally spawned and reared offspring of hatchery steelhead experienced greater mortality than offspring of wild steelhead during all three major life history stages, e.g., egg-to-fry, fry-to-smolt, and smolt-to-adult. These studies strongly suggest that adaptive differences occurred between hatchery and wild populations in a relatively short evolutionary time period.

Foraging Behavior

Starvation is a primary cause of poor post-release survival in hatchery fish. Miller (1952) believed the high mortality of hatchery cutthroat trout in his studies was due to starvation. Hochachka (1961) reached a similar conclusion after examining the stomach contents of wild and hatchery trout 28 days after release into a stream: the latter had less food in their stomachs and lower mean body weights. Reimers (1963) concluded that the continuous and eventually lethal weight loss he observed in hatchery trout resulted from their inability to compete or forage in the wild.

Sosiak et al. (1979) concluded that hatchery-reared parr of Atlantic salmon foraged less effectively than naturally reared parr for at least 2 months after being released into streams. The wild parr consumed more food and a greater diversity of organisms than their hatchery counterparts. In addition, the wild parr fed primarily on benthic organisms while the hatchery-reared fish concentrated on terrestrial and winged insects, suggesting that hatchery parr continue to feed at the surface even after release. O’Grady (1983) also found that hatchery-reared trout ate less than their naturally reared counterparts immediately after release.

Myers (1980) found that hatchery chinook salmon, examined shortly after their release, were inept foragers compared with wild fish. The average ratio of stomach content to body weight was more than three times greater in wild fish (5.7%) than in hatchery fish (1.7%). In addition, newly released hatchery fish appeared to be non-selective feeders; 67% of their stomach contents was indigestible algae compared with 84% of anchovy in the stomachs of wild chinook salmon. The dietary composition of their stomach contents only converged after extended residence in the estuary. This suggests that hatchery fish eventually learn to forage more efficiently, or that only the efficient foragers remain to be sampled after inept foragers starved.

At least two studies suggest that foraging differences between wild and hatchery strains of salmonids are partially innate. Mason et al. (1967) found that wild, hatchery, and hybrid strains of brook trout, reared from eggs in identical environments, exhibited different foraging behaviors. Wild-strain fish fed only from the bottom, hatchery fish readily fed at the surface, and hybrids exhibited intermediate behavior. Uchida et al. (1989) found innate differences in the foraging behavior of wild and domestic strains of the larvae of ayu reared under identical conditions. Again, the hatchery strain readily fed from the surface while the wild strains would not.

Other studies suggest foraging differences between wild and hatchery-reared fish are affected by conditioning. Johnson and Ugedal (1986) released hatchery-reared brown trout into a lake. Initially the fish fed on surface-dwelling prey but after several weeks of residency they were feeding on natural prey. In later analyses the diets of both wild and hatchery-reared trout were similar. The percentage of inedible and energetically unprofitable items eaten by the hatchery-reared trout decreased over time, suggesting that foraging efficiency can be improved with experience.

Regardless of rearing environment or strain, the experimental salmonids used by Bryan (1973) and Paszkowski and Olla (1985) always preferred live prey to commercial pellet diets. This suggests that prey movement is a primary cue stimulating prey attack behavior. Bryan (1973) found rainbow trout had an innate preference for live prey over pellets, but he also determined that fish developed weak and readily reversible training biases for familiar foods over novel foods. He concluded that cues other than familiarity were probably important in the natural foraging behavior of trout. Paszkowski and Olla (1985) demonstrated that experience with live prey improved the foraging performance of hatchery-reared coho salmon smolts challenged to feed on *Cragon spp.* However, even after repeated strikes, some smolts were never able to ingest large individuals even though they were within suitable size limits. Subsequently, Maynard et al. (1996b) documented improvements in foraging efficiency after live food training for chinook salmon.

In summary, all these studies on foraging behavior indicate that live food supplementation may be useful in training young salmon to handle live prey more efficiently. It may also prevent the fish developing dietary preference against natural feeds.

Social Behavior

Many studies have indicated that the hatchery rearing environment can profoundly influence social behavior of Pacific salmon, and social divergence of cultured fish may begin as early as the incubation stage. For example, the lack of substrate and high light levels which may occur in the hatchery incubation environment can induce excess alevin movement, lowered energetic efficiency, reduced size, and aberrant behaviors (Poon 1977, Leon and Bonney 1979, Mighell 1981, Murray and Beacham 1986, Fuss and Johnson 1988)**.** Food availability and rearing densities in hatcheries far exceed those found in natural streams, and may contribute to differences in agonistic behavior between hatchery- and wild-reared fish (Symons 1968, Bachman 1984, Uchida et al. 1989, Grant and Kramer 1990, Olla et al. 1990, Berejikian 1995a, Olla et al. 1998). Hatchery rearing environments may also deprive salmon of the psycho-sensory stimuli necessary to develop anti-predatory behavior fully (Olla et al. 1998).

Juvenile salmonids establish and defend foraging territories through agonistic contests, and levels of aggression have been positively associated with dominance in these contests (Egglishaw 1967, Fenderson and Carpenter 1971, Holtby et al. 1993, Berejikian 1995a). Both Fausch (1984) and Metcalfe (1986) found that dominant individuals tended to obtain more energetically profitable stream positions; hence, fish with relatively high levels of aggression may be expected to have a competitive advantage over less aggressive fish.

Evidence suggests that, although agonistic behavior has a genetic basis, it can be profoundly influenced by environmental (rearing) conditions. In comparative study of hatchery and naturally reared Atlantic salmon of common ancestry, Fenderson et al. (1968) and Fenderson and Carpenter (1971) found that agonistic activity of hatchery-reared fry was greater than that of naturally reared fry over a range of rearing densities, while wild fry were more aggressive at only the lowest densities. Bachman (1984) noted that hatchery-reared brown trout were equally successful in agonistic contests against wild brown trout in a natural stream, but hatchery trout abandoned their territories and moved more frequently among territories than did wild trout. Both Symons (1968) and Olla et al. (1990) deduced that an internal motivation, such as hunger, appeared to be positively associated with aggression, while Grant and Kramer (1990) concluded that territorial hierarchies can break down at high social densities.

Levels of aggression appear to differ between domesticated and wild populations, suggesting that genetically based changes can occur in a hatchery population after only a few generations of culture. Offspring from a domesticated brook trout population demonstrated higher levels of aggressive activity than offspring from a wild population when both populations were reared under similar hatchery conditions (Moyle 1969). Swain and Riddell (1990) observed that newly emerged, ‘socially-naïve’ coho salmon fry from two domesticated populations demonstrated significantly greater levels of aggression than fry from geographically proximate wild populations. In a companion study (Riddell and Swain 1991) aggression in coho salmon was found to be a heritable trait. The results of these studies demonstrate a genetic basis for the differences found between hatchery and wild populations.

Berejikian (1995b) suggested that newly emerged fry from a wild steelhead population initially had higher levels of aggression than fry from a locally derived, domesticated population. However, after several months of rearing, offspring of domestic steelhead were significantly more aggressive than offspring of wild steelhead when both were reared in food-limited and/or low-density environments (including a natural stream channel).

In summary, juvenile salmonids from domesticated and wild populations appear to demonstrate adaptive differences in agonistic behavior, and the behavioral development of domesticated and wild fish appears dependent upon their rearing environment.

Habitat Preference

Cultured and naturally reared salmonids are known to respond differently to habitat; in most cases wild fish utilize both riffles and pools in streams, while newly released hatchery fish primarily use pool environments similar to their raceway rearing experience. Using an artificial stream channel, Dickson and MacCrimmon (1982) observed that hatchery-reared Atlantic salmon parr persistently held positions higher in the water column than naturally reared parr from the same parent population. This indicated that the hatchery rearing environment caused a shift in habitat preference. In a study by Bachman (1984) hatchery brown trout released into a stream occupied foraging sites which were less energetically efficient than those used by wild trout, even though they frequently displaced wild trout from their sites. The hatchery trout also had higher energy costs as they constantly moved from site to site.

Hatchery strains are typically more surface-oriented than wild strains. The cultured Atlantic salmon parr observed by Sosiak (1978) swam closer to the surface and spent more time in contact with the surface than wild parr. Similarly, Mason et al. (1967) found hatchery strains of trout were more surface-oriented than wild strains reared from eggs in the same environment. Uchida et al. (1989) observed that larvae of wild ayu were found at greater depths than hatchery larvae reared and observed in the same environment.

In summary, with regard to habitat preference, most of the innate surface orientation of hatchery fish is probably an adaptive response to the common culture practice of introducing food at the surface of the water.

Response to Predators

Predation is a major factor affecting the post-release survival of hatchery-reared fish. Experimental evidence indicates that hatchery strains of salmonids have increased risk-taking behavior and lowered fright responses compared with wild fish. Surface feeding may condition hatchery fish to approach the surface of the water column (Uchida et al. 1989, Maynard et al. 1995, Olla et al. 1998), and this behavior increases their vulnerability to predators. Studies by Donnelly and Whoriskey (1991), and Maynard et al. (1996a) have also attributed increased vulnerability to predators to their decreased camouflage (crypsis) in stream environments caused by the monochrome concrete surroundings in the hatchery. The losses are significant. Ellis and Noble (1960) estimated 12-30% of the juvenile chinook salmon released from a hatchery on the Klickitat River were preyed on in the 40 miles between the hatchery and the Columbia River. Furthermore, the predators are selective. In the Chehalis River hatchery coho salmon are more vulnerable to predation by squawfish than wild coho salmon, as squawfish rarely feed on salmon smolts until the hatchery smolts are released (William Waknitz, NMFS, pers. commun., July 1991).

Other evidence indicates that hatchery strains are more vulnerable to predation than wild strains. Johnsson and Abrahams (1991) observed that offspring of crosses between wild steelhead and hatchery-strain rainbow trout were more willing to forage in the presence of a predator, an adult rainbow trout, than offspring of pure wild steelhead crosses. However, the hybrids were no better at avoiding predation in 15-second trials.

Increased risk-taking behavior without an increased ability to avoid predators may have put domesticated rainbow trout at greater risk than wild steelhead. In several experiments by Berejikian (1995b), the fry of wild steelhead from the Quinault River were better able to avoid the prickly sculpin than fry from a locally derived hatchery population. The fry were reared under laboratory conditions so that behavioral differences between the two populations were probably genetically based.

Fish which approach the surface of the water column have been shown to increase their risk to avian predators (Kramer et al. 1983). Therefore, the surface orientation of cultured fish, and their tendency to approach large moving objects at the surface, exposes them to the predators such as herons, mergansers, and kingfishers, etc. Mason et al. (1967) reared both hatchery and wild strains of brook trout in raceways and observed that the wild strain fled humans while the hatchery strain trout approached them. The tendency of hatchery fish to approach large moving objects is partly innate.

Patten (1977) and Olla and Davis (1989) have shown that fright responses are at least partially a conditioned behavior. In similar studies with cultured cod, Nordeide and Svassand (1990) observed they approached larger cod more slowly and less closely than wild cod cohorts did. The investigators speculated that, as cultured fish experienced more cannibalism in their artificial rearing environment, they were more conditioned to be cautious with larger cod.

In laboratory trials Bams (1967) observed that naturally reared sockeye salmon fry were less susceptible to predators than hatchery-reared fry. This susceptibility was inversely related to the proportion of time alevins were reared with gravel in their incubation baskets. In these studies, the vulnerability to predation was size-related and, as the fry reared in baskets without gravel were smaller, he concluded that the rearing environment was responsible for increased predation on hatchery fry.

Morphological and Physiological Differences

Taylor and Larkin (1986) developed a discriminate function model using morphometric measurements to distinguish between hatchery and naturally reared coho salmon parr. In addition to having a different shape, juvenile hatchery reared fish were less variable than naturally reared parr. They concluded that these differences were under environmental rather than genetic control. Bams (1967) and Taylor and McPhail (1985) indicated that hatchery-induced morphological differences affected swimming speed and therefore the ability to escape predators.

Jarvis (1990) determined that predator-naive Atlantic salmon smolts facing a new osmotic environment suffered more severe physiological stress when predators were present than did smolts previously exposed to predators. These, and other morphological and physiological divergences between natural and hatchery-produced fish may significantly influence post-release survival.

Reproductive Behavior

Hatchery practices have altered reproductive behavior by relaxing selection pressure on secondary sexual characteristics used in breeding competition in the wild, while increasing selection pressure on primary sexual characteristics. Fleming and Gross (1989) concluded that relaxation of breeding competition in the hatchery has led to the evolution of female coho salmon with less well developed kypes and breeding colors than their wild counterparts. The hatchery strains studied expended energy in developing larger and more numerous eggs than equivalent size members of the wild stocks from which they were derived.

Fleming and Gross (1992) found that the reproductive behavior of male coho salmon differed between hatchery and wild strains. Hatchery-strain males allowed to spawn naturally were less aggressive and generally less active than wild-strain males. It appeared that the relaxation of competition among males for access to females in the hatchery, coupled with the possibility of sperm competition which may have occurred as a result of hatchery spawning techniques, resulted in hatchery-strain males investing disproportionate amounts of energy towards testes production. The authors concluded that investing energy for sperm production, rather than in secondary sexual characteristics that aid in obtaining access to females, was only a disadvantage to hatchery-strain males spawning naturally in the presence of wild-strain males. Similarly, Berejikian et al. (1997) observed that adult captive reared coho salmon were less reproductively fit than their wild counterparts. In the absence of competition, hatchery-strain males would probably breed as successfully as wild-strain males.

Either inadvertently or intentionally, hatcheries usually develop strains which spawn at different times than their ancestral stocks. Studies by Salo and Bayliff (1958), Ricker (1972), and Hager and Hopley (1981) have all demonstrated a genetic basis for spawning time. Hatcheries often inadvertently select for early run timing by spawning a disproportionately higher percentage of earlier returning fish. From a management perspective, the advantage of this temporal separation is that it minimizes interbreeding between domestic and wild stocks, which is generally believed to be harmful to wild populations (Reisenbichler and Rubin, In press). The disadvantage is that the progeny of feral-spawning domestic strains emerge prior to peak abundance of natural aquatic invertebrate blooms, and thus suffer high mortality rates (Nickelson et al. 1986).

Conclusions

Artificial culture environments condition salmonids to respond to food, habitat, conspecifics, and predators in a different manner than do fish reared in natural environments.

Present culture techniques also alter selection regimes, which may result in genetic divergence between hatchery and wild populations. The phenotypic differences observed between cultured and wild fish are both genetically and environmentally controlled. The affects of hatchery reared fish on the population abundance of wild fish are discussed in Section III which follows.

III. IMPACTS OF ARTIFICIAL PRODUCTION RELEASES ON WILD FISH

A. Production Strategies

1. Supplementation Projects

The use of hatcheries to supplement wild stocks is a controversial topic in the Pacific Northwest. Unfortunately the information on supplementation projects is confusing. Over 60 separate supplementation projects have been proposed yet they appear to use different definitions of supplementation, different interpretations of objectives, and different evaluations of success.

Smith et al. (1985) defined supplementation as the release of fish from hatcheries at locations away from the hatchery to increase natural production in streams determined to be seeded or used at less than optimal levels. Miller et al. (1990) defined it as the planting all life stages of hatchery fish to enhance wild/natural stocks of anadromous salmonids. Steward and Bjornn (1990) were the most specific, describing it as the provision of surplus harvests of fish from stocks which may not otherwise naturally produce sufficient fish to meet the demand from fishermen. Management opportunities range from rebuilding threatened or endangered wild stocks to bolstering already self-sufficient natural runs. Hatchery fish used to supplement wild stocks of salmonids are stocked at egg, fry, fingerling, smolt, and adult life-stages.

The definition used in the Regional Assessment of Supplementation Projects (RASP 1992) was more pertinent to the relevance of ecological and genetic factors in the milieu of the species involved. Consequently the RASP definition is adopted by the contributors to this document, viz:

> *Supplementation is an attempt to maintain or increase natural production while maintaining the long-term fitness of the target population, and keeping the ecological and genetic impacts on non-target populations within specified biological limits.*

Using this definition, a successful supplementation project would have to meet the following three criteria:

- Did the project maintain or increase natural production?
- Did the project maintain the long-term fitness of the target population?
- Did the project keep the ecological and genetic impacts on non-target population within specified biological limits?

A project which does not meet all three tests must be judged to have failed.

A more practical definition of supplementation has been given by Cuenco (1993), viz:

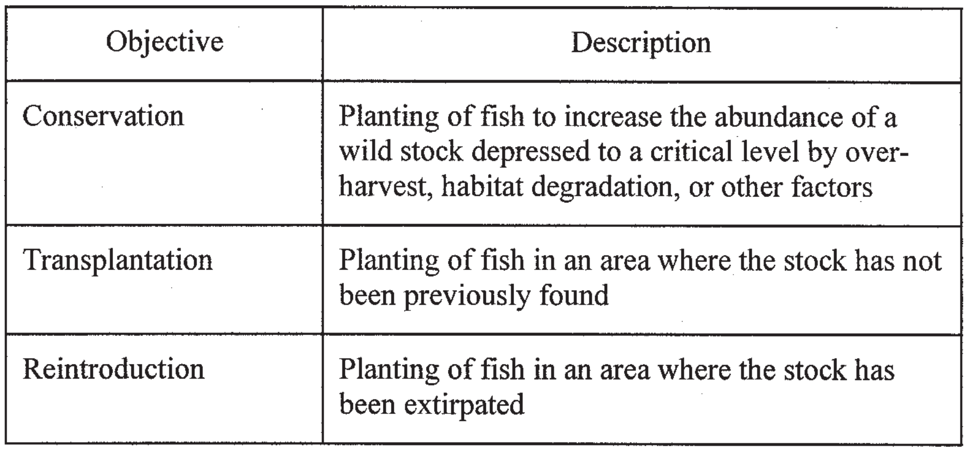
> *Supplementation is the stocking of fish into natural habitat to increase the abundance of naturally reproducing fish populations.*

Even though the RASP (1992) definition of supplementation is probably the most widely accepted, in reality, this simple definition by Cuenco (1993) is what is actually implied.

Because of variability in year-to-year salmon returns and field sampling limitations, defining the contribution of supplementation to wild populations is not a simple task. The relationship of genetic changes in target and non-target populations to population fitness is a subject of controversy. There is still significant ambiguity regarding both definitions as it is not specified whether the increase in population must continue after supplementation ceases.

The objectives of supplementation

The objectives of supplementation are threefold. These are conservation, transplantation, or reintroduction. Their general parameters are summarized in Table 2.



Objective	Description
Conservation	Planting of fish to increase the abundance of a wild stock depressed to a critical level by over-harvest, habitat degradation, or other factors
Transplantation	Planting of fish in an area where the stock has not been previously found
Reintroduction	Planting of fish in an area where the stock has been extirpated

In the Pacific Northwest most supplementation projects have the objective of conservation or reintroduction of a specific anadromous salmon stock. The transplantation of anadromous salmon either within or outside their natural range is not now a common objective.

The use of supplementation

Cuenco (1993, 1994) provided guidelines for deciding when to initiate supplementation of a population. He believed four conditions were required:

- The wild populations were declining
- Sufficient spawning habitat was available and underused
- Other actions which could address the cause(s) of population declines could not be implemented in a timely manner
- Hatchery technology and facilities were available to increase stock productivity above replacement

The decision to use supplementation is complex. This is evident from a brief review of some special cases. For example, the potential for supplementation to increase the population of fish spawning in the wild depends strongly on the stock productivity. Stock productivity is the number of adult fish which one generation contributes to the next. According to Cuenco (1994), a stock productivity <1.0 means the population is decreasing; >1.0 means it is increasing, and =1.0 means it is stable. For large populations, the stock productivity can decline <1.0 for relatively long times without the population going extinct. Small populations have less time. Salmon populations are characterized by extreme variation in year-to-year adult returns, and it is not uncommon for healthy populations occasionally to experience stock productivity < 1.0.

Under most conditions, if stock productivity for the wild stock is consistently less than the replacement, then a supplementation program will not result in a self-sustaining wild population. The population may increase during the supplementation phase due to higher contribution from the hatchery program, but when supplementation is terminated the population will continue to decline because the reasons for the low survival have not been corrected.

There is one potential exception to this result. Due to predatory and competitive impacts a population can be ‘trapped’ in a lower stability region (Peterman 1977) or extinction vortex (Soulé 1986). Supplementation can increase stock productivity by itself if it is large enough to move the population into a high stability region. In this situation the size of the supplementation project and release protocols are critical; for example, if heavy predation is a cause of low density then release of larger groups of fish would increase survival (Fresh and Schroder 1987; Supplementation Work Group 1999).

When stock productivity is consistently <1, a supplementation program must be viewed as an interim measure to maintain a population temporarily until environmental conditions change or anthropogenic impacts are corrected. While supplementation may have some negative impacts on wild fish these are preferable to extinction.

Supplementation is not needed for a depressed stock with productivity >1, as it should be able to recover on its own. A supplementation program may increase the population size above some critical level more rapidly and therefore accelerate recovery.

The risk in using supplementation

A generalize decision tree for supplementation is presented in Figure 1. The first decision is whether or not to use supplementation. When the probability of extinction is high, the choices may be limited to:

(a) starting a supplementation program,
(b) starting a limited captive brood program to maintain genetic integrity (Flagg and Mahnken 1995), or
(c) letting the population go extinct.

But, as noted previously, there is significant uncertainty in the predication of extinction risk. Therefore, the basic trade-off in the start of a supplementation program is balancing the risk of extinction (outcome 2 in Figure 1) against a decrease in the long-term fitness of the population (outcome 14).

There is a significant difference of opinion of the risk and benefits of supplementation (Sterne 1995). One view favors widespread use of supplementation while another favors reduced hatchery intervention. The former is influenced by the desire to recover the runs as quickly as possible (Sterne 1995), while the latter is concerned that attention is diverted from the real issues behind population decline and the potential impacts of hatchery programs on the long-term fitness of the populations. Waples (1991) noted that the potential impact of hatchery releases on wild stocks included direct genetic impacts, indirect genetic impacts, and ecological impacts.

The controversy is fueled by the fact that many proclaimed impacts of supplementation are not based on experimental work with Pacific salmon, but with other species, and even plain theory. This is because the experimental work needed to confirm the genetics impacts of salmonid supplementation are extremely costly and may require 5-10 years or more to complete.

The dynamic of a hypothetical supplementation project is illustrated in Figure 2 as a function of time. The overall project is divided into three time periods:

(1) pre-supplementation with a declining population,
(2) supplementation, and
(3) post-supplementation.

The figure does not include all the different outcomes presented in the supplementation decision tree (Figure 1). This figure is the basis for discussion of the general characteristics of a supplementation project.

The statistics of supplementation are quite complex and obviously specific to any project. Nonetheless some fundamental questions about supplementation projects in general need to be addressed. For example:

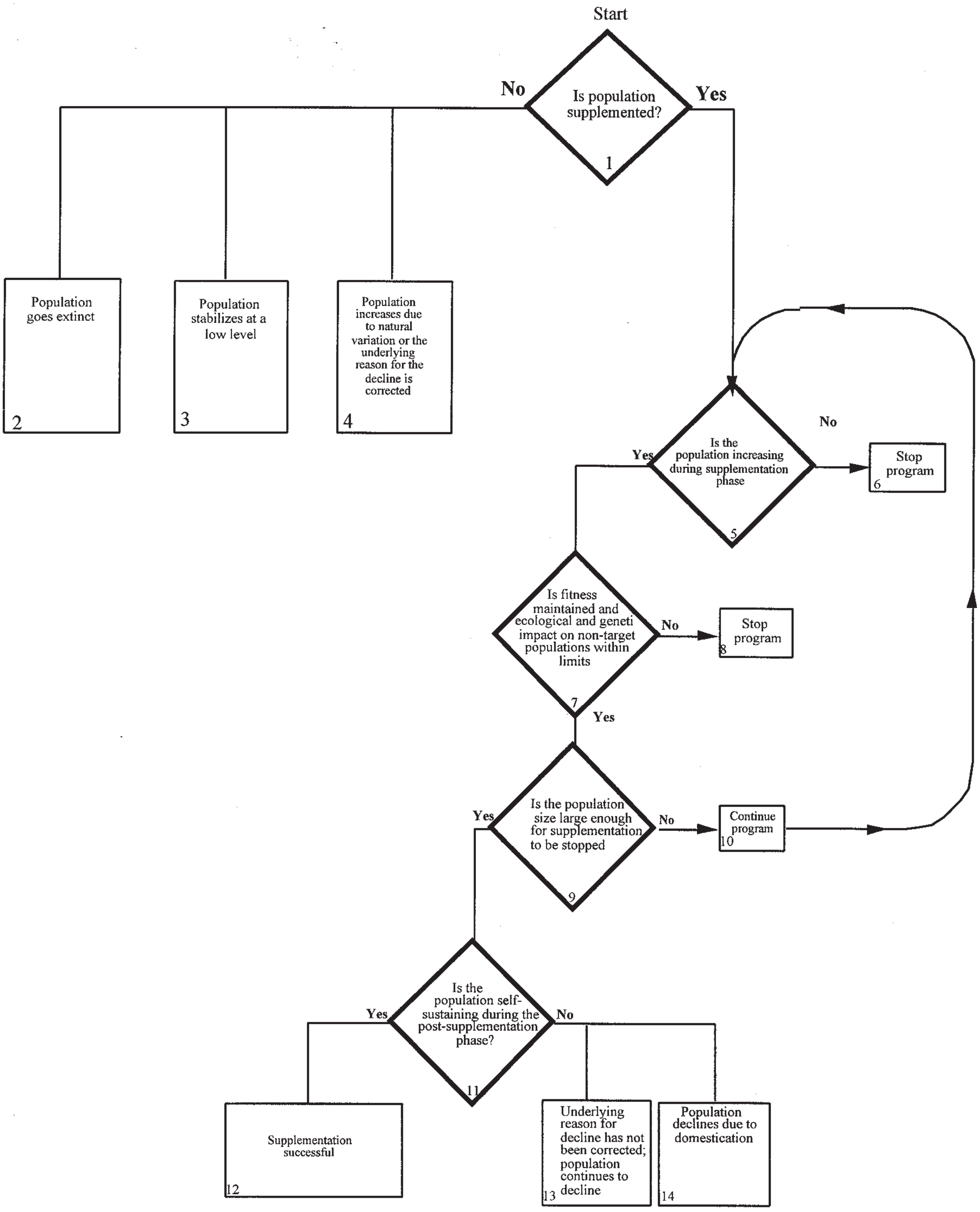


Figure 1. Generalized decision tree for supplementation.

- How long does supplementation have to be conducted before the population increases?
- How long does supplementation have to be conducted before the population increase can be detected (Decision 5, Figure 1)?
- How long does supplementation have to be conducted before impacts on fitness of the target population or ecological and genetics impacts on non-target stocks can be detected (Decision 7)?
- How long does the supplementation project have to last (Decision 9)?
- After supplementation stops, how long is needed to determine if a population is self-sustaining (Decision 11)?

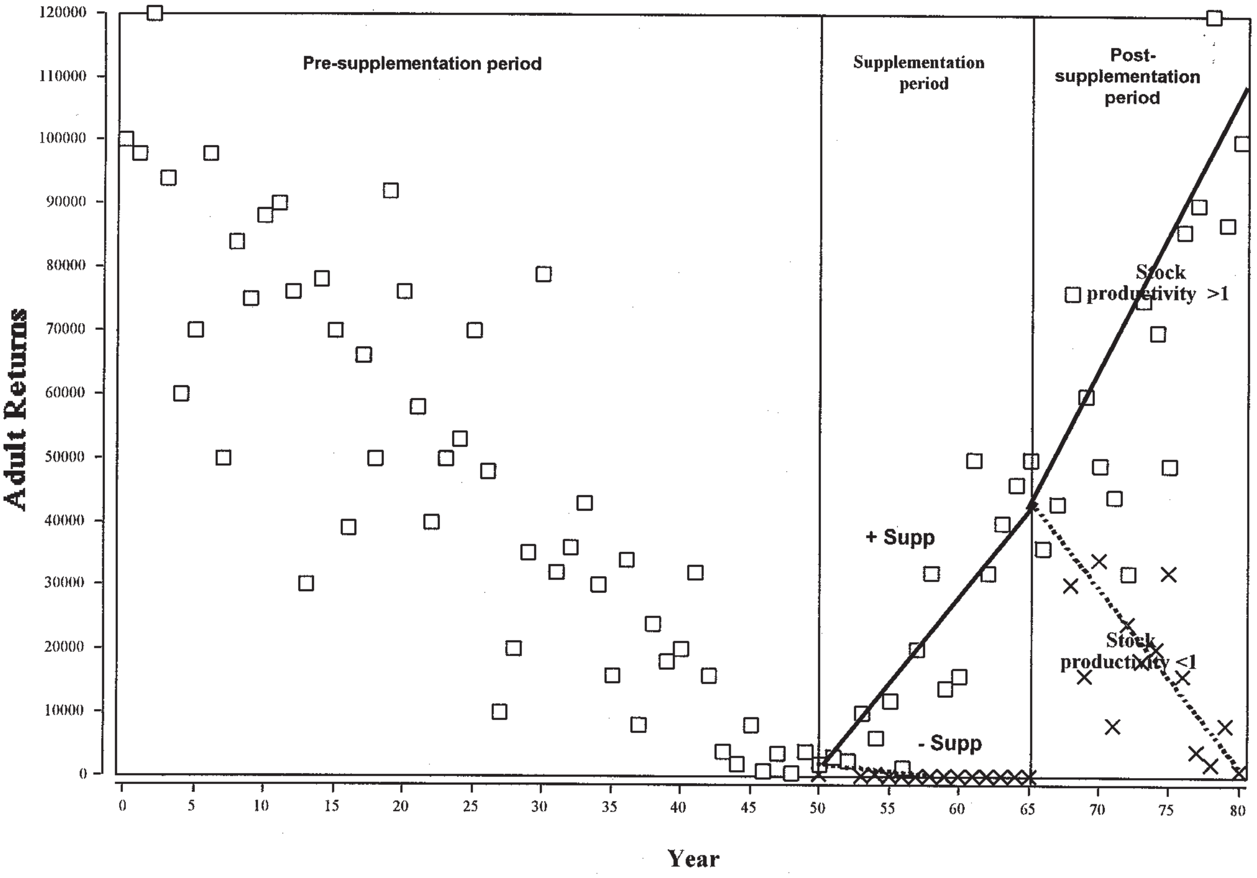


Figure 2. Dynamics of a hypothetical supplementation project.

In general, the success of a supplementation project can only be determined after the planting of hatchery fish has stopped (Decision 11). A successful supplementation program should result in a self-sustaining population. In the special case where the stock productivity is consistently <1 it could also be argued that an increase in population can be considered a success (Decision 5). In this case the alternative to not supplementing the stock is extinction.

The length of time to detect a statistical change in escapement depends on the variability of the escapement, the accuracy of the escapement estimates, and the degree of certainty needed (Peterman 1990, Korman and Higgins 1997). Based on a Monte Carlo simulation Korman and Higgins (1997) found that there was generally less than a 50% chance of detecting a population response unless the population change was large (more than a twofold increase) or the post-treatment monitoring period was long (>10 years). Statistical power was improved by increasing the precision of the escapement estimate. Lichatowich and Cramer (1979) found that 20 to 30 years of escapement data may be needed to produce an 80% chance of detecting a 50% change.

For discussion purposes it is assumed that 10-15 years of supplementation and 10-15 years of post-supplementation monitoring will be needed. Therefore, the total time required to evaluate a project is 20-30 years. Due to the length of time needed for statistical testing it may be difficult to differentiate the impacts of supplementation from those arising from changes in the freshwater or ocean conditions. This issue as it relates to genetic monitoring has been reviewed by Hard (1995).

An evaluation of some previous supplementation projects

A number of past supplementation projects were judged to be successful within their definition of the term and their specific goals. The individual objectives of these projects were primarily introduction, and they were frequently associated with the removal of upstream barriers. Those successfully resulting in self-sustaining populations are summarized in Table 3.

Table 3. Supplementation projects resulting in self-sustaining populations.

State/Providence	River/Lake	Species	Years Since Planting Ended	Reference
Washington	Lake Washington	Sockeye	60	Withler 1982
Alaska	Frazer Lake	Sockeye	26	Withler 1982
Minnesota, Ontario, Michigan & Wisconsin	Lake Superior	Lake trout	Only 10 of 47 management zones still stocked	Schreiner and Schram 1997

It is relevant to note here that the historic long-distance transplants of salmonids, for example, to South Africa and New Zealand, etc., are not considered supplementation projects within this section. Information on these inter-basin programs can be found in Withler (1982) and Fedorenko and Shepherd (1986).

There are two important listings of successful supplementation projects. Miller et al. (1990) reviewed 316 supplementation projects, of which only 26 fitted their definition of supplementation. Twenty-five of these projects were considered a success by the project managers, but only 18 were subjected to quantitative evaluation. The authors concluded that none of the evaluated projects had rebuilt natural runs to self-sustaining levels. Using their more restrictive definition of supplementation, RASP (1992) concluded that none of these projects qualified as supplementation projects at all. At issue was the evaluation of the genetic impacts of supplementation on the population itself. Therefore, RASP concluded, supplementation had neither been attempted nor evaluated.

Chilcote et al. (1986) found the reproductive success of hatchery fish spawning in the wild was only 28% of the value for wild fish. The basis for this reduction in reproductive success was thought to be selective pressures from conventional spawning or rearing protocols.

Reisenbichler and McIntyre (1977) planted eggs or un-fed fry in natural streams from hatchery x hatchery, hatchery x wild, and wild x wild crosses. In the wild, wild x wild crosses had the highest survival.

Nickelson et al. (1986) found that stocking of large pre-smolts contributed little to rebuilding the population. The hatchery population used in this work spawned much earlier than the wild fish (probably due to hatchery practices). When these fish returned to spawn their eggs and emergent fry were subjected to high flows and scour. They concluded that fish used for supplementation should be the same size as wild fish and spawn at the same time.

Reisenbichler (1988) found that the further coho salmon were transferred, the lower their smolt-to-adult ratio (relative to the smolt-to-adult ratio at the release hatchery). Therefore, local broodstock is much more desirable than out-of-basin broodstock.

There are many supplementation projects currently being conducted all over the Pacific Northwest. Some major ongoing projects are listed in Table 4. However, those with adequate monitoring and evaluation programs, or have operated long enough to produce results, are surprisingly small in number. Information on three current supplementation projects is presented in Appendices A-C.

Fundamental assumptions of supplementation

Supplementation from an ecological point of view is based on two assumptions:

- The production of smolts is limited by one or more of the following reasons: (a) escapement of adults to the basin, (b) spawning area, (c) egg to alevin survival, or (d) alevin to smolt survival
- There is the carrying capacity (space and food) for additional fish in the basin

If either assumption is incorrect then there is no reason to believe that supplementation will increase the number of salmon spawning in the wild.

Table 4. Major ongoing supplementation projects.

Title	Area	Species	Initial Release of Fish
Summer Chum Supplementation Project	Hood Canal, WA	Summer chum	1999*
Yakima/Klickitat Fisheries Project	Yakima/Klickitat basins, WA	Chinook	1998
Idaho Supplementation Studies	Salmon and Clearwater basins, ID	Chinook	1991-2
Umatilla Satellite and Release Sites Project	Umatilla basin, OR	Fall chinook, spring chinook, steelhead	1995*
Nez Perce Tribal Hatchery Project	Clearwater basin, ID	Spring/summer chinook	2001*

* Some releases occurred prior to this time but were not part of the formal experimental plan.

Assessing carrying capacity of a stream is more difficult than is generally assumed. RASP (1992) noted, “One cannot assume that a stream that previously supported a now-depleted abundant and productive salmon population has vacant habitat equivalent to the difference between the past and present populations.” Even in the most isolated headwaters the carrying capacity may be significantly less than historical levels due to interventions, such as mining, logging, construction of splash dams, elimination of beaver dams, removal of other channel obstructions, and grazing. These have all contributed to changes in channel morphology (water depth, complexity, etc.), water temperature, water flow, and energy flow. Many of these changes may have occurred more than a century ago.

Returning adults are important contributors of nutrients and energy to the spawning and rearing conditions in the freshwater environment. First, during redd-building they disturb the gravel. Although this may result in egg loss from older redds, removal of fine sediments improves overall egg survival (McNeil and Ahnell 1964) and displaced salmon eggs are an important energy input to the stream (Kline et al. 1995). Second, if the adults are not directly consumed by predators, the disintegrating carcasses are absorbed in one of four ways (NRC 1996). They may be fixed autotrophically by aquatic plants and subsequent transfer through periphyton-based food webs; fixed heterotrophically by bacteria and fungi and transfer through decomposer-based food webs; taken up abiotically by sorption within the stream substrate, and consumed directly by fish and other aquatic organisms. Cederholm et al. (1989) concluded that the ability of streams to retain carcasses has been greatly reduced by removal of low water dams, rocks, and reducing the complexity of the river channel and riparian zone. The benefit of large numbers of adult spawners in excess of those needed for alevin production has not been recognized by salmon harvest managers.

The importance of carcasses in the nutrition of salmon has been illustrated recently by Kline et al. (1995) in Alaska, and Larkin and Slaney (1997) in British Columbia. For some stocks, up to 91% (mean = 61%, range 27-91%) of the nitrogen in the smolts was of marine origin, i.e. carcasses and eggs. The availability of carcasses and eggs to pre-smolts may be especially important in winter and early spring when other food is scarce.

Another consequence of fewer returning adults is the decrease in quality of the gravel with the accumulation of sediments. Interventions, such as logging, farming, and construction, continuously add to input of sediments. In addition, the body size of many stocks has been declining due to selective pressures, hatchery practices, declining ocean productivity, density-dependent affects of large hatchery releases, or a combination of any of these factors (Weitkamp et al. 1995). Smaller-sized fish produce fewer eggs and are less able to make long spawning migrations. Van den Berghe and Gross (1984) found that nest depth was strongly correlated with female size, therefore eggs from smaller females are at more risk from scour and redd superposition by later spawners.

The solution, however, is not planting larger numbers of fry or fingerling. This in itself will not result in a significant increase in adult returns if the cumulative lack of spawners and carcasses over time has destroyed the productivity and base of the food chain in the inter-gravel spawning and rearing environment. Consequently one recent supplementation project in the Willapa River area included carcass addition to support stream-side egg boxes. However, it is likely this practice will have to be repeated over many years to develop the productivity to historic levels. Unfortunately, the necessary background information to identify the levels of intervention is typically lacking.

Finally, supplementation projects have been largely viewed as hatchery projects and have been staffed with hatchery or evaluation biologists. In practice they are multi-disciplinary projects, requiring specialists in fields such as benthic ecology and food chain productivity.

Practical problems of supplementation programs

Supplementation programs have evolved from traditional production hatchery programs. The full impact of the change in objectives from production to supplementation has not been reflected in any real changes in hatchery operations or facilities. Some of the most serious practical problems are discussed below.

(i) Location of the weir - Selective collection of broodstock is a serious problem in many supplementation projects. Bugert (1998) listed six criteria for effective broodstock collection. These were:

- An ability to collect only the targeted populations for supplementation
- A capability to capture all age-classes of the target populations without injury or stress
- An equal collection efficiency during both peak and nadir of the hydrograph
- An ability to sort marked (hatchery) and unmarked (natural) salmonids

- Unimpeded passage of non-targeted species and populations and, at times, most of those fish in the targeted populations
- Compatibility with federal designated ‘wild and /or scenic’ rivers (PL 90-542,82)

Some of these criteria are in conflict, especially for high-elevation and high-gradient streams. For example, a weir which meets the first four criteria is likely to impede the passage of non-target fish, and may not be compatible with ‘wild and scenic’ legal restrictions. Consequently, Bugert (1998) recommended less reliance on a single-objective, single-location collection strategy.

(ii) Location of release sites - Acclimation ponds are widely used with supplementation projects even though there is little data to show any cost-effectiveness. Bugert (1998) listed four criteria for the use of acclimation ponds:

- The site must be accessible in early spring (and winter if possible) to transfer fish from the hatchery. Continuous access is required to feed and maintain the health of fish, prevent vandalism, and remove debris or slush accumulations at pond intakes
- The site must be far upstream to ensure proper homing and spawning distribution within the supplemented watershed
- The site must often use river water which is non-consumptive, and preferably gravity-fed as power may not be available. Supplemental groundwater may be required to temper river water in winter and spring if ice accumulation is a problem
- The site must meet development standards of ‘wild and/or scenic’ rivers (PL 90-542,82) and any local jurisdictions

Again some criteria are in conflict. The first, for example, favors acclimation sites low in the basin while the second favors those high in the basin. Electrical power lines for pumped surface water or groundwater are usually more available low in the basin, and it is always easier to site a facility with a pumped water supply.

(iii) The life history patterns of released fish - In cases where all the salmon have been extirpated from a basin then a donor stock has to be used for supplementation. Reisenbichler (1988) showed that, for coho salmon, the transfer distance is inversely related to smolt-adult survival. Therefore, nearby local stocks are preferred to those introduced from the edge of the basin, or even greater distances.

At many hatcheries spawning is ended once the required number of eggs for that stock is obtained. This practice results in the selection for early spawning fish which, in some cases, can advance the mean spawning time by 2-3 months (Flagg et al. 1995b). Nickelson et al. (1986) found that for production operations this advance had little impact on post-release survival, but if the fish were used for supplementation then their progeny might be exposed to adverse environmental conditions. Therefore this resulted in little contribution to the wild population. As hatchery fish are typically larger than wild fish, because of (a) selection for the early portion of the run, (b) use of warmer groundwater for incubation and early rearing, and (c) artificial feeds, the authors concluded that larger hatchery fish can dominate smaller wild fish causing their emigration or death. They recommended that hatchery fish used for coho supplementation should be released at a size similar to the local wild fish. In addition, the life history patterns of the hatchery fish should be similar to the wild stock.

In summary, with reference to all these case studies, the following conclusions might be drawn about ‘successful’ supplementation projects:

- There are examples of successful supplementation projects which have resulted in self-sustaining populations. On the other hand more examples have not.
- The impacts on fitness of the targeted stock, and the genetic and ecological impacts on non-targeted stocks, have been largely ignored.
- The level of monitoring and evaluation has not been adequate in many of the past and current supplementation projects.
- It is impossible to determine if a self-sustaining population has resulted because hatchery fish are still being released.
- Until 10-15 years of post-release data are collected, the use of supplementation as a management tool to maintain or increase natural production cannot be fairly judged.

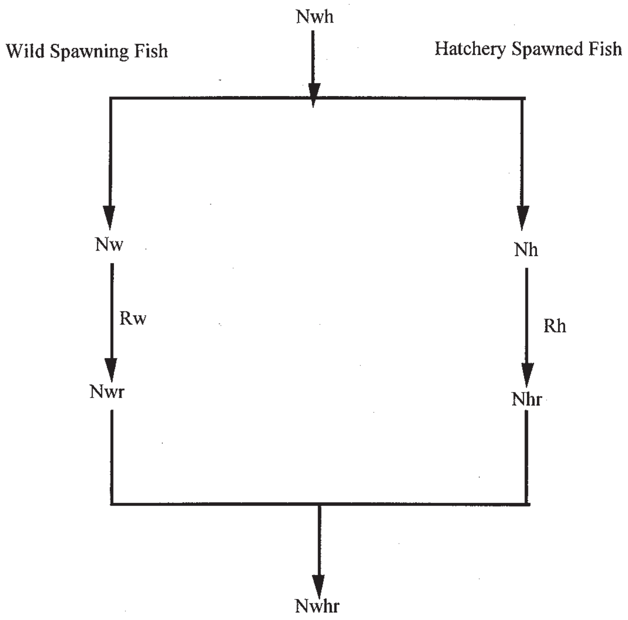
Supplementation Models

There have been a number of attempts to model the impact of supplementation on population dynamics (Byrne et al. 1992; Cuenco, 1994; RASP, 1991) and genetics (Hard, 1995; Waples & Do, 1994).

A generalized model of combined stock abundance and productivity of a supplementation project is presented in Figure 3a for year 1 of an internal supplementation program (using local broodstock). The figure is based on nomenclature used by Cuenco (1994). Figures 3b-3d are based on one possible classification scheme. Different authors have made fundamental assumptions about which lineage of fish to be followed, and their fitness in relationship to the original wild stock. In many cases there is little experimental evidence to support one set of assumptions over another.

In Figure 3a the total number of adult fish is equal to Nwh. Of this number of fish, some are taken into the hatchery and reared (Nh). The total number of recruits is equal to Nwhr and comprise of Nwr (from the wild) and Nhr (from the hatchery). The biological cycle is repeated with the Nwhr becoming the Nwh for the next generation. Once hatchery fish start to return the model becomes more complex (Figure 3b). In both the wild and the hatchery there are three different combination of spawning fish (wild x wild, hatchery x wild, and hatchery x hatchery).

A critical question is the rapidity with which the hatchery influence on fitness diminishes with each successive generation of natural spawning and whether or not progeny of hatchery-reared parents ever approach the fitness of their native counterparts (RASP 1991). If the progeny of wild x wild, wild x hatchery, hatchery x hatchery mated with wild fish in F2 and F3 generations, the following combinations result (Table 5):



Nwh = Total abundance of spawners
Nh = Number of fish spawned in the hatchery
Nw = Number of fish spawning in wild
Rh = Hatchery productivity (recruits/spawner)
Rw = Wild productivity (recruits/spawner)
Nhr = Number of recruits produced from hatchery fish
Nwr = Number of recruits produced from fish spawning in wild
Nwhr = Total number of recruits

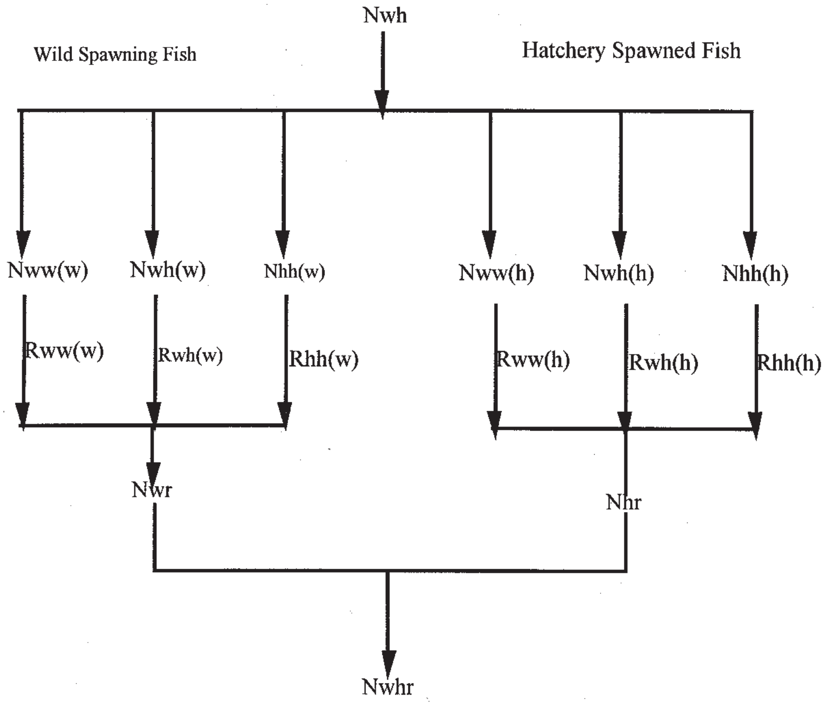
Figure 3a. Year 1 of an internal supplementation program.

Table 5. Possible permutation of crosses with successive generations (F1 - F3)

F1	w x w	w x h	h x h
F2	(w x w) x w	(w x h) x w	(h x h) x w
F3	(w x w) x (w x w)	{(w x h) x w} x w	{(h x h) x w} x w

If the supplementation project continues long enough, there may come a time when it is impossible to differentiate the parentage of the fish (Figure 3c). The hatchery would still produce more recruits/spawner because of higher early survival.

The test of supplementation occurs when the hatchery program is terminated (Figure 3d). Is the stock productivity of the wild fish >1, and greater than that which would have occurred if the stock had not been supplemented? It is probably not valid simply to compare the pre-project stock productivity (R_w in Figure 3a) with the post-supplementation value ($R_{mix,w}$ in Figure 3d) due to potential environmental changes.



Nwh = Total abundance of spawners
Nww(h); Rww(h) = Number of wild x wild fish spawned in the hatchery; recruits/spawner
Nwh(h); Rwh(h) = Number of wild x hatchery fish spawned in the hatchery; recruits/spawner
Nhh(h); Rhh(h) = Number of hatchery x hatchery fish spawned in the hatchery; recruits/spawner
Nww(w); Rww(w) = Number of wild x wild fish spawning in the wild; recruits/spawner
Nwh(w); Rwh(w) = Number of wild x hatchery fish spawning in the wild; recruits/spawner
Nhh(w); Rhh(w) = Number of hatchery x hatchery fish spawning in the wild; recruits/spawner
Nhr = Number of recruits produced from hatchery fish
Nwr = Number of recruits produced from fish spawning in wild
Nwhr = Total number of recruits

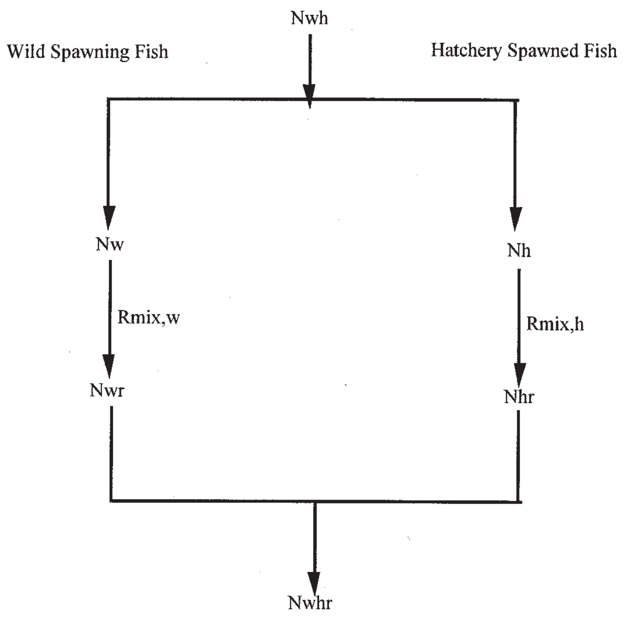
Figure 3b. Internal supplementation program after hatchery fish return.

For any one of the different crosses in the wild, it is possible to write a simple equation for stock productivity, viz:

$$\frac{N_{whr}}{N_{wh}} = (\%\ \text{Female})(\%\ \text{Spawning})(\text{Egg / Female})(\text{Egg / Smolt})(\text{SAR})$$

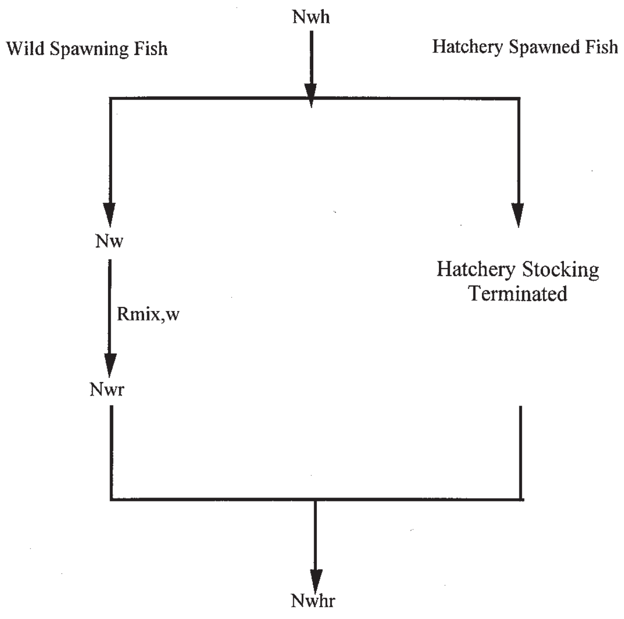
Where % Female = Percent females in populations
% Spawning = Percent of female that successfully spawn in the wild
Egg/female = Number of eggs per female
Egg/smolt = Percent egg-to-smolt survival
SAR = Percent smolt-to-adult survival

Additional research on the comparison of hatchery and wild fish with respect to mate selection and spawning and egg-to-fry survival is needed. The source of broodstock used for supplement projects should be subject to much more analysis and discussion.



Nwh = Total abundance of spawners
Nh = Number of fish spawned in the hatchery
Nw = Number of fish spawning in wild
Rmix,w = Recruits/spawner for wild spawning fish
Rmix,h = Recruits/spawner for hatchery spawned fish
Nhr = Number of recruits produced from hatchery fish
Nwr = Number of recruits produced from fish spawning in wild
Nwhr = Total number of recruits

Figure 3c. Year n of an internal supplementation program.



Nwh = Total abundance of spawners
Nw = Number of fish spawning in wild
Rmix,w = Recruits/spawner from fish spawning in wild
Nwr = Number of recruits produced from fish spawning in wild
Nwhr = Total number of recruits

Figure 3d. Post-supplementation phase of an internal supplementation program.

The future operation of supplementation hatcheries

Supplementation has been largely viewed as a fisheries management practice with important genetic components. Ecological impacts and husbandry requirements have been viewed with much less importance.

In production hatcheries there is an overwhelming emphasis on producing fish of uniform size and adhering rigidly to size and time-of-release goals. The practice of volitional release is simply not possible because of the demands on the facilities. Therefore hatchery operations themselves impose major selective pressures on the stock. These domestication pressures can be adaptive for hatchery rearing but may be very non-adaptive for fish that must spawn in the wild.

A stock used in a supplementation project should have a life history as varied as wild stocks (Bugert, 1998). The maintenance of genetic diversity through broodstock selection and fertilization protocols is well developed, but little attention has been given to genetic diversity through their subsequent life history protocols.

Potential aspects of hatchery operations for supplementation projects might include the following:

- Broodstock collection throughout the seasonal run, and maintenance of differences in resulting size until release
- Reduction in rearing density to allow survival of slower growing fish. This might also require variation in feeding levels between different raceways
- True volitional release and multi-year rearing cycles for some species of fish
- Use of surface water supplies to maintain normal growth patterns
- Use of natural environment rearing components (NATURES), predation training, and exercise
- Natural mate selection and natural incubation systems
- Use of substrate and reduced light levels in artificial incubation (if used)
- Modification of production diets and/or natural food items

Implementation of some of these rearing strategies may require significant additions in capital costs and operational costs. There might also be some reduced production.

Conclusions

1. Supplementation can maintain a population until underlying causes of decline are corrected.
2. The genetic impacts of supplementation can be minimized with appropriate broodstock collection, fertilization, and rearing protocols.
3. Monitoring and evaluation of most older supplementation projects is inadequate. At least five major projects with appropriate monitoring and evaluation plans are underway in the Pacific Northwest. All are still in the supplementation period. The response of these populations in the post-supplementation period is unknown at this time.

4. The fitness of supplementation fish can be improved with more appropriate rearing and release protocols. The use of conventional rearing protocols significantly reduces success.
5. The use of out-of-basin stocks or highly domesticated hatchery stocks is highly undesirable.
6. Because of the high variability of adult escapement estimates, 10-15 years of data (or more) is needed to determine if the population has increased or decreased. Alternative monitoring parameters are needed for estimating the impacts of supplementation.

2. Conservation Hatchery Protocols

Introduction

It is clear from the preceding section that attempts to use supplementation to rebuild naturally-spawning populations of Pacific salmon have yielded poor results so far. One of the reasons is that production hatchery fish do not have the same capacity to survive as their wild cohorts, as they are generally different in behavior, morphology, and physiology. The solution, and the challenge, is to develop protocols which produce fish from hatcheries with ‘wild-like’ attributes, thereby reducing impacts on wild fish and increasing survival. In this section, the potential impacts of artificial propagation on the biology and behavior of fish are first summarized, and then conservation hatchery strategies to help mitigate the unnatural conditioning provided by hatchery rearing are discussed.

Potential impacts of hatchery rearing

Hatcheries figure prominently in the management of Pacific Northwest salmon fisheries. For the most part, hatcheries have been successful in producing fish for the fishery (Mahnken et al. 1998). However, hatcheries and hatchery management practices have often worked to the detriment of wild fish (Waples 1991, Flagg et al. 1995b, NRC 1996, Waples 1999). Present hatchery practices are geared toward mass-production under unnatural conditions. These have been described in Section III.A.1, above.

Although the protective nature of hatchery rearing increases egg-to-smolt survival, it has been reported for many years (Greene 1952, Miller 1952, Reimers 1963) that post-release survival and reproductive success of cultured salmonids are both considerably lower than that of wild-reared fish. Hatchery practices which induce genetic changes (domestication, etc.) are often considered prime factors in reducing fitness of hatchery fish in natural ecosystems (Reisenbichler and McIntyre 1977, Nickelson et al. 1986, Goodman 1990, Waples 1991 and 1999, and Hilborn 1992). Rearing practices which disrupt innate behavioral responses may also play a major role in reduced performance of hatchery fish after release.

Behavioral deficiencies in released animals have been cited as causes of failure to re establish wild populations by, among others, Gipps (1991), Johnson and Jensen (1991), DeBlieu (1993), and Olney et al. (1994). Current fish culture techniques may be imparting similar behavioral deficiencies in hatchery reared salmon. Studies by Maynard et al. (1995) indicated that the hatchery rearing environment can profoundly influence social behavior of Pacific salmon, and social divergence of cultured fish may begin as early as the incubation stage. Poon (1977), Leon and Bonney (1979), Murray and Beacham (1986), and Fuss and Johnson (1988) demonstrated that lack of substrate and light levels of the hatchery incubation environment induced excess alevin movement, lowered energetic efficiency, reduced size, and, in some wild stocks, death. Similarly, as food availability and rearing densities in hatcheries far exceeded those of natural streams, Symons (1968), Bachman (1984), and others have all concluded that such factors contributed to differences in agonistic behavior between hatchery- and wild-reared fish.

Work by Olla et al. (1998) suggested that hatchery rearing environments deprived salmon of the psycho-sensory stimuli necessary to develop anti-predator behaviors fully. Maynard et al. (1995) reviewed information indicating that hatchery strains of salmonids have increased risk-taking behavior and lowered fright responses compared with wild fish. These authors, together with Uchida et al. (1989) suggested that surface feeding conditioned hatchery fish to approach the surface of the water column, thus increasing their susceptibility to avian predation.

Maynard et al. (1996a) and Donnelly and Whoriskey (1991, 1993) also attributed increased vulnerability of hatchery fish to predators to decreased crypsis (camouflage coloration) for stream environments. This lack of camouflage coloration is caused by the monochrome background of the (concrete) rearing environments of the hatchery raceways.

Finally, Allee (1974), Dickson and MacCrimmon (1982), Berejikian (1995a), and others, have demonstrated that cultured and naturally-reared salmonids respond differently to habitat. In most cases, for example, wild fish utilized both riffles and pools in streams while newly released hatchery fish primarily used pools. The pool is more similar to a raceway environment.

Reisenbichler and Rubin (In press) summarized the current situation by concluding that, ".. the only similarities in hatchery and wild environments for salmonids are water and photoperiod." Almost every other component of the hatchery rearing environment, such as food, substrate, density, temperature, flow regime, competitors, and predators, etc., differed from those naturally experienced by wild fish. Consequently, the National Research Council (NRC 1996) and, more recently, others (Anders 1999, Flagg and Nash 1999, Waples 1999,) have suggested that operational strategies of production hatcheries can be changed to conservation strategies for the protection of wild stocks. A number of hatchery strategies for the conservation of Pacific salmonids are discussed below. A complete array of conservation hatchery strategies are fully described in Flagg and Nash (1999).

The concept of the conservation hatchery

The strategic role of a conservation hatchery is to promote restoration of wild stocks of fish. This requires fish rearing be conducted in a manner that mimics the natural life history patterns, improves the quality and survival of hatchery-reared juveniles, and lessens the genetic and ecological impacts of hatchery releases on wild stocks.

It has been recommended (SRT 1998, Flagg and Nash 1999) that conservation hatcheries:

- determine spawning, hatching and emergence times of the local population, and duplicate these in the hatchery by controlling water temperature to natural profiles
- use low rearing densities and base their goals for growth and size at emigration on natural population parameters
- simulate growth rate, body size, and body (proximate) composition by controlling water temperature, diet composition, and feeding rates
- have incubation and rearing vessels with options for habitat complexity to produce fish more wild-like in appearance, and with natural behaviors and higher survival
- provide prerelease training experiences, such as forage conditioning and antipredator conditioning which, while many yet are still theoretical, are beginning to show improved survival and fitness.

Important factors effecting quality of hatchery reared fish include:

Rearing density – Rearing density is one of the most important and well-studied factors affecting fish quality. Westers and Copeland (1973) and Maheshkumar (1985) found that the fin condition of Atlantic salmon deteriorated with increasing rearing densities. Soderberg and Meade 1987), however, indicated there was no relationship with fin condition, growth, or in-culture survival at rearing densities of 8.5 to 68.7 kg/m^3 (0.53 to 4.29 lbs/ft^3). Reftsie (1977) demonstrated that both growth and condition factor of rainbow trout are inversely related to rearing density.

Inverse relationships between rearing density and growth, condition factor, and food conversion efficiency have been observed in coho salmon by Fagerlund et al. (1981). In addition, coho salmon reared at high densities suffered greater physiological stress as measured by body water content, fat and protein contents, inter-renal cell nuclear diameter, and mortality rates. For coho salmon smolts, Wedemeyer (1976) discovered that rearing densities as low as 16 kg/m^3 (1 lb/ft^3) induced physiological stress. Pitano et al. (1986) found increased rearing densities reduced levels of plasma thyroid hormones, and Banks (1992) found they reduced levels of gill ATPase levels.

In a survey of 85 variables related to strain and culture conditions by Homer et al. (1979), only the five associated with either water flow, amount of living space, or relative water level in rivers explained the post-release survival of Atlantic salmon. Unpublished data by Sandercock and Stone (cited in Fagerlund et al. 1981) indicated that the adult return of coho salmon appeared to be inversely related to rearing-pond density, although this was not totally confirmed in work by Hopley et al. (1993).

Martin and Wertheimer (1989) examined the effect of low, intermediate, and high rearing densities on the post-release survival of chinook salmon. In the hatchery, all four rearing densities showed similar high survival (99.5% or greater), but fish reared at higher densities were smaller at release. The low density group showed the highest adult return (1.0%), followed by the two intermediate-density groups (0.9 and 0.7%) and the high density group (0.6%).

However, the increased number of smolts produced at the two higher densities compensated for their reduced return rate and yielded a higher number of adult returns per unit volume of rearing space.

These and other studies with chinook salmon (Hopley 1980, Fagerlund et al. 1987, Denton 1988, Downey et al. 1988, Banks 1990) have shown a consistent inverse relationship between rearing density and percentage of fish surviving to recruit to the fishery and spawning area. However, in most cases the greatest number of adults per unit volume can still be produced by rearing fish at intermediate densities. Some interesting relationships were found when data were combined by species. For example, the SAR for chinook tended to decrease with increasing rearing density, but for coho little relationship could be found. The adult yield for coho salmon increased with increasing density, while the adult yield for chinook remained constant. Until further data are available, lowered density indices as proposed by Banks (1994), and Ewing and Ewing (1995) of 0.08-0.15 lb/ft^3/in for spring and fall chinook salmon, and between 0.30-0.40 lb/ft^3/in for coho, should used in attempts to maximize adult return.

Enriched rearing habitats – Research on higher vertebrates has shown that simple and practical (habitat enrichment) changes to the way animals are kept and grown can have beneficial effects on their physiology as well as their behavior (Gipps 1991). Providing animals with more complex rearing habitats which approximate natural conditions is an increasingly popular method for improving the well being of animals in zoos. In many cases, behavioral repertoires may be recovered even after many generations of absence simply by recreating the correct environmental stimuli. These habitat enrichment techniques, according to Johnson and Jensen (1991), DeBlieu (1993), Olney (1994), and others, may also have application to salmonid hatchery populations.

Fish culturists have long recognized that fish reared in earthen-bottom ponds have better coloration than those reared in concrete vessels (Piper et al. 1982). However, only recently has it been understood that rearing salmonids over natural substrates, similar to those over which they will be released, increases survival by enhancing cryptic coloration. Research by Fuji (1993) indicates these morphological color changes can take weeks to complete, as pigments and chromatophore units are developed to match the general background. The cryptic coloration ability generated by these long-term stable color adaptations appears to reduce detection by predators. Donnelly and Whoriskey (1991) found that brook trout reared for 11 weeks over distinct background colors were significantly less vulnerable to predators when challenged over background colors similar to those over which they were reared.

Prolonged work by Maynard et al. (1995, 1996a, 1998b) with salmonids reared in natural rearing enhancement systems, which promote full development of the morphological camouflage pattern needed after release, showed that survival was increased. In these systems (called NATURES) the complexities of the experimental artificial rearing habitats simulate the release habitats. Substrates were configured in several ways, using sand, gravel, artificial corrugated inserts, or painted patterns. Every effort was made to match the color of the substrate (which produces the cryptic coloration patterns in fish) to that of the receiving-stream environment to produce body camouflage patterns (fish crypcisity) most likely to reduce vulnerability to predators. In these studies, the in-stream post-release survival of fish reared in NATURES were compared with the survival of fish reared in conventional hatchery tanks. The results of the studies are briefly summarized below:

- 1991-1992. Fall chinook salmon were reared from swim-up to smolt in 400-L raceways fitted with cover, structure, and substrate. Relative post-release survival to a collection weir about 2 km downstream was about 50% higher (40 versus 60%; P=0.007) for NATURES fish.
- 1994. Spring chinook salmon were reared for 3 months in 400-L raceways fitted with cover, structure, and substrate. Relative post-release survival to a collection weir about 225 km downstream was about 23% higher (22 versus 27%; P<0.05) for NATURES fish under clear water conditions, but not in turbid water conditions (34 versus 31%; P=0.285).
- 1994. Fall chinook salmon were reared hatchery from swim-up to smoltification in pilot scale 5,947-L raceways fitted with cover, structure, substrate, and an underwater feed delivery system. Relative post-release survival to a collection weir about 20 km downstream was 26% higher (38 versus 48%; P=0.001) for NATURES fish.
- 1997. Fall chinook were reared to smolt for about 3 months in 18,000-L production scale raceways fitted with cover, structure, and substrate at a WDFW hatchery. Relative post-release survival to a collection weir about 20 km downstream was similar (69% each) for both groups.
- 1998. Fall chinook were reared to smolt in the 18,000-L raceways. Relative post-release survival to a collection weir about 20 km downstream was 11% higher (60 versus 67%; P<0.001) for NATURES fish.

These results suggest that in-stream post-release survival of fish reared in these special habitats is significantly greater than that of their counterparts reared conventionally. Consequently, although not yet documented, it is assumed that survival to adulthood will be improved. The studies in 1997 and 1998 included components to evaluate ocean returns, but the data will not be available for a number of years.

In conclusion, it appears habitat enrichment strategies can aid in the production of ‘wild-like’ hatchery fish more suited for enhancement programs than fish reared in conventional systems.

Forage training – Foraging theory suggests that supplementing standard pellet diets with live foods will profoundly increase post-release foraging ability of cultured fish. Field trials generally confirm that live-food supplemented diets improve the post-release foraging ability and survival of cultured fish. Gillen et al. (1981) found that previous experience in capturing live prey enhanced the foraging behavior of tiger muskellunge by decreasing the time and number of strikes required to capture natural live prey. Johnson (1978) found that tiger muskellunge reared in the hatchery on a live fish diet had higher post-release survival than their cohorts reared only on pellets. Similarly, Hesthagen and Johnsen (1989) demonstrated that brown trout reared in earth-bottom ponds with natural food supplementation had a higher post-release survival than control trout reared in tanks and fed only pellets.

Maynard et al. (1996b) investigated the use of live-food supplementation to increase the post-release foraging ability of hatchery-reared fall chinook salmon. Trained salmon were found to feed on twice the number of familiar and novel prey as untrained fish. In addition, even though food was abundantly supplied to both treatment groups, the growth and natural coloration of fish reared on the live-food supplemented diet was better than that of fish fed only pellets. These and other studies suggest that live-food supplementation can increase the post-release foraging ability of hatchery-reared fish. However, rearing fish in semi-natural habitats with natural foods may not always enhance survival, as observed by Mundie et al. (1990) in a study with coho salmon.

Anti-predator conditioning – Studies on salmonids carried out over many years have demonstrated an increase in post-release survival of juveniles following anti-predator conditioning in hatchery vessels. Thompson (1966), working in a natural stream, demonstrated that post-release survival of chinook salmon smolts exposed to electrified predator models was greater than unconditioned smolts, and Kanayama (1968) reported improved post-release survival of chum salmon after similar conditioning.

More recently, juvenile salmonids from wild and hatchery populations were shown to exhibit differences in predator avoidance behavior (Johnsson and Abrahams 1991) and ability (Berejikian 1995a, 1995b). This suggested genetic basis for these traits. However, the ability of juvenile salmonids to avoid predation improved with experience.

Laboratory studies by Patten (1977), Healey and Reinhardt (1995), and others, demonstrated that anti-predator behavior and predator avoidance ability of juveniles of several salmon species improved following exposure to actual predation events. Suboski (1988) and Olla and Davis (1989) suggested that anti-predator conditioning involved various combinations of visual, olfactory, and auditory stimuli, all of which could trigger innate anti-predator responses. Brown and Smith (1997 and 1998) and Berejikian et al. (1999) demonstrated that conditioning by a combination of injured con-specific predator odors in the absence of visual and auditory stimuli improved subsequent predator recognition and avoidance behavior in rainbow trout and chinook salmon, respectively.

The use of predator avoidance training as tool to increase the post-release survival of chinook salmon has been investigated by Maynard et al. (1998a). Fall chinook salmon reared in pilot scale raceways were exposed to limited predation by birds (great blue heron and hooded merganser) and fish (largemouth bass and brown bullhead). The in-stream post-release survival of the conditioned fish was 26% higher than naive controls.

In conclusion, these studies suggest anti-predator training can be used to increase the post-release survival of hatchery-reared fish. There is no evidence that anti-predator conditioning has a detrimental effect on post-release survival.

Reintroduction strategies

A number of potential reintroduction strategies have been suggested for progeny reared in conservation hatcheries. There appears to be no clear information on the outcome to fitness from varying release strategies but it seems reasonable that conservation hatcheries should release smolts at a size which equals the size distribution of smolts in the wild population. The greatest risk of releasing oversized hatchery fish is that they will out-compete smaller wild fish. For a long time it has been known that, in intra specific contests over food and space, all else being equal, the largest fish usually wins (Hoar 1951, Chapman 1962, Mason and Chapman 1965, Abbot et al. 1985).

Fish from conservation hatcheries should be released on their own volition, and out-migrate during windows for natural downstream migration. The key to volitional release, assumed by NRC (1996), Brannon et al. (1982), Kapuscinski (1997), is that fish will not leave the hatchery until certain physiological processes, such as smoltification, trigger their downstream migratory behavior. The need is to provide windows of opportunity for out-migration which mimic time and age patterns found in the wild populations. Within these windows, fish may leave if they wish or remain behind to fend for themselves and smolt, residualize, or perish as natural selection takes it course.

Conservation hatcheries should therefore adopt practices to reduce straying to no more than 5% (Grant 1995). According to Sholes and Hallock (1979), Labelle (1992), Unwin and Quinn (1993), Pascual et al. (1995), Dittman et al. 1995), and others, juvenile salmon must experience the odors of their natal system at various times and physiological states when they can be learned to maximize imprinting opportunity. Conservation hatcheries should, therefore, rear fish for their entire juvenile freshwater lives in water from the intended return location. When this is not possible, a period of acclimation on intended return water should improve imprinting and homing and reduce straying. Conservation hatcheries should program their releases to accommodate the natural spatial and temporal patterns of abundance in wild fish populations and release numbers should not exceed carrying capacities of (freshwater and oceanic) receiving waters.

Even though there appears to be no clear information on the outcome to fitness from varying release strategies, adhering to these guidelines should markedly decrease negative effects of hatchery releases on the wild fish population.

Conclusions

A number of conservation hatchery type rearing protocols can be used to improve fitness and survival of hatchery fish. For some strategies, such as NATURES rearing, there is good evidence of a potential range of survival increase. For many other strategies, no clear ‘improvement’ range has yet been described. Nonetheless, most proposed conservation hatchery strategies combine sound conservation principles and basic salmon biology. They are common sense approaches to increasing the quality of hatchery fish. It would not appear optimistic to conclude that, using a combination of conservation hatchery protocols, the survival of hatchery fish could be improved by 50-100% or greater, while reducing the ecological impacts of the release.

B. Competition

Introduction

The following section reviews what is known about the potential for competition between hatchery and wild reared chinook salmon and steelhead trout.

When salmonids harm one another in contests over limiting resources they are considered, in general, to be in competition (Birch 1957, Horner and Bjornn 1976). This competition may occur when fish fight for feeding territories, displace one another from critical hibernation habitat, graze down estuarine food resources before other fish can utilize them, monopolize available mates, or dig up the redd of another fish.

If contests between fish populations are over limiting resources, as required for true competition to occur, then a density dependent relationship will exist in which increases in one population will produce decreases in the growth, survival, etc., of the other. Conversely, if resources are not limiting, competition does not occur, and the relationship between the growth and survival of the two groups will be density independent. It is this density dependent relationship that most biologist use to conclude that inter-specific competition is occurring between salmonids. Thus Hearn (1987) suggested inter-specific competition may be occurring between salmonids in a watershed when the decline of one species is accompanied by a concomitant increase in another. However, it should be remembered that this may be a casual rather than causal relationship, with factors other than competition responsible for the relationship between the two populations.

Intra-specific competition occurs more often and has greater severity than inter-specific competition because there is greater niche overlap between members of a species than individual of different species (Fraser 1969, Lonzarich 1994, Fresh 1997). When species evolve sympatrically their niche requirements tend to diverge, which further reduces the potential for inter-specific competition between them. Therefore when groups (morphs, life history strategies, races, or species) which have evolved sympatrically are introduced or reintroduced into a common habitat, then competition is generally less intense between them than groups which have evolved allopatrically (Hearn 1987).

By definition, hatchery and wild reared salmonids will not compete unless they require the same limiting resources. Thus, the modern enhancement strategy of releasing chinook salmon and steelhead trout as smolts markedly reduces the potential for hatchery and wild fish to compete for resources in the freshwater rearing environment. Miller (1953), Hochachka (1961), and Reimers (1963), among others, have noted that this potential for competition is further reduced by the fact that many hatchery salmonids have developed different habitat and dietary behavior than wild salmonids. If similar ecological divergence has occurred in Snake River salmonids, for example, it may further alleviate the potential for competition between wild and hatchery fish in the migratory corridor, estuary, and marine environments.

It has been suggested by Fresh (1997) that competition is most likely to occur between hatchery and wild salmonids in the estuarine and near-shore environments where food resources are limited, and the fish become concentrated on their way to the open ocean. However, as little is known about salmonid behavior and ecology in these habitats, it is difficult to determine if hatchery and wild salmonids are actually competing for limited resources. Even for coho salmon in the Oregon Production Index (one of the better studied populations) McNeil (1991) believed there was no clear cut density dependent relationship between hatchery and wild fish which indicated that competition is occurring in the marine environment. Although studies by Fresh (1997) and others have shown that hatchery fish can disrupt the growth, survival, and abundance of native salmonid communities in streams, the role of competition in causing these changes is unclear. Further, these results of presmolt competition in the territorial freshwater-life stage cannot be readily extended to the schooling migratory marine-life stage of most post-smolt hatchery and wild salmonids.

The following review mostly concerns competition between wild and hatchery reared steelhead trout and spring-summer chinook salmon. The review is broken down into three sections, namely the intra-specific competition between wild and hatchery-reared chinook salmon; the intra-specific competition between wild and hatchery-reared steelhead trout, and the inter-specific competition between chinook salmon and steelhead trout.

Wild and hatchery-reared chinook salmon

Snake River spring-summer chinook salmon typically rear at least one summer in streams and then undergo a fall downstream migration to hibernation areas, where they hibernate in suitable bottom rubble that protects them from predators and displacement. In the spring they emerge from hibernation, resume feeding, and then migrate downstream as yearling smolts about mid-spring. Edmundson et al. (1968) demonstrated that summer chinook salmon fry in their natal streams during their first spring maintained a permanent station which they aggressively defended during the day and abandoned at dusk when they moved into quieter inshore waters to shelter.

Everest (1969) observed that the microhabitat used by chinook salmon in streams changed as the fish grew, with larger fish seeking deeper and faster water. Just after emergence from the gravel the fry resided in quiet shallow water over a variety of substrates ranging from silt to 20 cm rubble. Spring chinook fry exhibiting a territorial life style tended to be closely associated with substrate, while those fry living in hierarchical social groups preferred to live in quieter water where they swim up to 0.8 m above the substrate. Some yearling fish (precocious males) remained in freshwater and spawned about the time they turned two years old. Larger yearling precocious males which remained in freshwater for a second year utilized deeper water microhabitat than under-yearling chinook salmon (Everest and Chapman 1972). They believed suitable over-wintering habitat was the primary limiting factor for presmolt chinook salmon in freshwater.

When yearling (spring) chinook salmon begin their down-river migration they utilize different habitat than both hatchery and wild under-yearling (presumably fall) chinook salmon. Dauble et al. (1989) observed that, in general, under-yearling fall chinook salmon remain close to the shore, while yearling spring chinook salmon tend to migrate down the mid-river channel. These and other investigators (Richards and Cernera 1989, Roper and Scarnecchia 1996,) noted the downstream migration of chinook salmon was temporally separated, as hatchery chinook salmon migrated downstream at different times of day than wild chinook salmon.

It is unclear whether or not hatchery and wild chinook salmon utilize similar or different resources in the estuarine environment. The best available information comparing the use of estuarine resources by the two rearing types is primarily based on ocean-type (fall) chinook salmon data. In a study by Fisher and Pearcy (1989) in Coos Bay, Oregon wild and hatchery fall chinook salmon were generally found to utilize the same habitat at the same time. Spring chinook salmon released from a hatchery were found to be both spatially and temporally separated from these fish. In addition the hatchery spring chinook salmon collected in Coos Bay were found in large aggregations suggesting migratory behavior, while both the hatchery and wild fall chinook salmon were more evenly distributed indicating they were residing in the estuary.

In contrast to the Coos Bay study, hatchery and wild chinook salmon in the Campbell River estuary were found by Levings et al. (1986) to display little habitat overlap. When released into the estuary hatchery fish were much larger than wild chinook, which resulted in their utilization of deeper water habitat than the wild chinook fry in seawater. In addition to being spatially separated, the two rearing types utilized the estuary for different lengths of time, with wild chinook residing in the estuarine environment for two months and hatchery fish only one month. Therefore there was little dietary overlap. In a later study by Brown et al. (1987), wild and hatchery fish were both found to eat calanoid and harpacticoid copepods, amphipods, and cladocerans in the estuary. However, hatchery fish alone were found to feed on cumaceae, while wild fish only fed on insects and decapod crustaceans. Although there was some dietary overlap it was not complete, and therefore the two types may not be in competition if they are foraging in different microhabitats. Levings et al. (1986) concluded that competition between wild and hatchery fish was not occurring as the release of hatchery fish did not appear to reduce the residence time of wild fish, and there was no evidence of a density dependent relationship between the two rearing types.

Korman et al. (1997) found some later evidence of competition between wild and hatchery chinook salmon in the Campbell River estuary. There was again spatial separation with wild chinook salmon having the greatest density in the estuarine zone sites, while the density of hatchery chinook salmon was highest in the transition zone sites. In addition, both groups showed different seaward emigration patterns. However, the peak abundance of wild and hatchery chinook in the estuary did coincide, and there was some indication of a density dependent relationship between the two rearing types indicating that competition was occurring.

Myers (1980), working in Yaquina Bay, found the dietary overlap of hatchery and wild chinook salmon changed over time. Initially after release from the hatchery there was little overlap, but as time passed the diet of hatchery chinook began to approximate more closely to that of wild chinook salmon. Although there was some habitat overlap between the two rearing types, wild chinook tended to be more abundant in the upper estuary, while hatchery chinook were more abundant in the lower estuary. Again this data, which is primarily on fall chinook salmon, suggests some competition may be occurring between wild and hatchery fish in that estuary.

Further information on competition between hatchery and wild chinook salmon is not available until the life-stages of reproduction. Chebanov and Riddell (1998) observed no noticeable difference in the morphology of ocean ranched and wild chinook salmon. When hatchery and wild chinook salmon were placed in test enclosures the wild males generally dominated hatchery males. However, quite unexpectedly, hatchery females dominated the wild females and obtained the preferred spawning sites. As wild male preferentially spawned with wild females and ranched males choose to spawn with ranched females, ranched fish of both sexes were the more successful spawners. It should be noted that there was some mating crossover with wild males also spawning with ranched females. The authors explain the unexpected reproductive advantage experienced by hatchery females as an artifact of the conditions the fish were held in prior to testing. However, if the experimental findings are valid and hatchery fish stray onto wild salmon spawning areas they may well compete with them for spawning sites.

Bjornn (1978) studied the effect of supplementation releases of chinook salmon fry on chinook salmon production in the Lemhi River. Unfortunately his study lacked controls and provided no observations on the in-stream behavior of hatchery and naturally produced salmon, and therefore provides little information on intra-specific competition. He did observe that the growth rate of chinook salmon fry was density dependent, which suggests that intra-specific competition is occurring at this life stage. In another supplementation study by Hillman and Mullan (1989), the release of 0-age hatchery-reared spring chinook salmon fry into the Wenatchee River system resulted in the displacement of naturally-reared spring chinook salmon fry. Both these studies and general theory on intra-specific competition suggest that planting spring chinook salmon fry will produce some level of competition with any naturally rearing chinook salmon they may encounter.

Intraspecific competition between wild and hatchery reared chinook salmon most likely occurs when they share the same microhabitat and dietary needs. This is a function of both when, where, and how hatchery fish are released, as well as the microhabitat and dietary preferences shown by the two rearing types. The less hatchery fish share the habitat and dietary requirements of wild fish, the less likely the two forms are to compete. Thus the release of spring chinook salmon fry into habitat with resident wild chinook salmon has great potential for producing competition between the two rearing types. In contrast, the release of well imprinted and rapidly migrating spring chinook salmon smolts from hatcheries which are geographically separated from wild fish rearing and spawning areas may generate very little competition between wild and hatchery reared chinook salmon.

A summary of the studies on intra-specific competition between wild and hatchery-reared chinook salmon is given in Table 6.

Table 6. Studies observing competition between wild and hatchery reared chinook salmon.

Study	Stage	Freshwater rearing	Migration corridor	Estuary	Ocean	Adult migration	Spawning
Dauble et al. 1989	smolt		unk-none				
Fisher and Pearcy 1988	smolt			unk-none			
Roper and Scarnecchia 1996	smolt		unk-none				
Levings et al. 1986	smolt			unk-none			
Brown et al. 1987	smolt			unk-neg			
Korman et al. 1997	smolt			unk-neg			
Myers 1980	smolt			unk-neg			
Chebanov and Riddell 1998	spawner						unk-neg
Bjornn 1978	fry	unk-neg					
Hillman and Mullan 1989	fry	unk-neg					
Gut feeling using good hatchery rearing and release protocols	smolts	none	none	minor	minor	none	none

Wild and hatchery-reared steelhead trout

Most summer steelhead trout in the Snake River spend three growing seasons in freshwater. Each fall the fish seek hibernation cover in their rearing area or migrate downstream to areas with suitable bottom rubble. In the spring the fish emerge from the rubble and resume feeding in their rearing areas. Steelhead fry, like chinook, maintained a permanent station which they defended aggressively during the spring and summer, according to Edmundson et al. (1968). At night they abandoned these territories and moved into quieter inshore waters where they shelter overnight.

Age-0 steelhead prefer shallow quiet water a few feet from shore. They are strictly territorial bottom dwellers intimately associated with large rubble substrate. As they grow they continuously shift their distribution into deeper and faster water. Thus age-1+ steelhead are found in deeper faster water towards the center of the stream. They are also territorial and intimately associated with the substrate. Everest (1969) noted they are typically found over larger rubble than age-0 steelhead. He concluded that suitable over-wintering habitat was the primary limiting factor for presmolt steelhead trout production in freshwater. Chrisp and Bjornn (1978) stated that summer steelhead trout must be at least 140-160 mm in length before they begin to smolt and migrate to the sea.

Both steelhead trout and rainbow trout are two life history strategies of a single species. According to Barnhart (1991) and Smith (1991) this makes it impossible for investigators to distinguish morphologically or behaviorally between the fry while they are rearing in streams. Because of their physical similarity and the high likelihood that they share similar freshwater habitat and feeding strategies, intra-specific competition between the two life history types has been included in this review.

The planting of hatchery steelhead fry into wild rainbow-steelhead habitat generally produces some form of competition between the two rearing types. When hatchery-reared steelhead trout fry were planted by Allee (1974) into artificial stream channels containing a resident population of wild steelhead trout the wild fry emigrated from the channel. He concluded that the hatchery fry remained in the channel not because they socially dominated the wild steelhead, but rather because they tolerated greater intra-specific rearing densities than the wild fry. When hatchery fry were released into a stream of the Quinault River system by Berejikian (1995a) they also displaced the wild fry from the most heavily utilized stream habitat. Bjornn (1978) released large numbers of hatchery reared steelhead fry into Big Spring Creek for over a decade. Although the significance of the results is weakened by the lack of controls, he observed that the release of hatchery steelhead trout fry markedly reduced the resident rainbow trout population over time. Over-wintering habitat, rather than food, appeared to be the limiting resource for this Snake River steelhead-rainbow trout population. It appears from all these studies that the release of steelhead fry into streams negatively affects wild steelhead fry rearing in the area whether competition occurs or not.

The planting of catch-size rainbow-steelhead trout in a habitat with an established wild trout population can produce an impact ranging from negligible to severe. When catch-size hatchery rainbow trout were stocked in the Madison River, Montana by Vincent (1987) he noted a dramatic decrease in the wild trout population. After the planting ended the natural population took four years to recover its original level. Although the author collected no supporting data, he attributed the wild population decline to hatchery fish disrupting the social structure of wild trout.

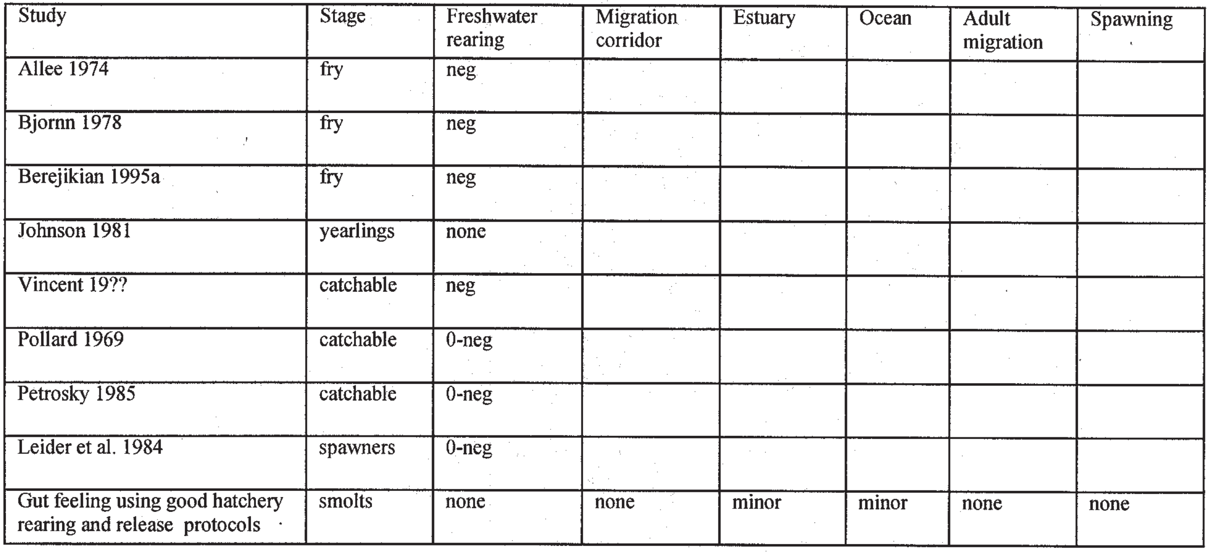
In Idaho streams, stocking catch-size rainbow trout had only a minor impact on the wild steelhead trout population. Although Pollard (1969) and Pollard and Bjornn (1973) found that the stocking of hatchery trout depressed the wild fish population temporarily, it rapidly returned to pre-stocking levels within two weeks. Even though hatchery trout were observed to displace wild steelhead from their feeding positions, they were usually found to prefer deeper and faster water than the age-0 and age-1 steelhead. This produced good microhabitat separation between the hatchery and wild reared trout. Competition between the two was further reduced by hatchery rainbows feeding less readily on floating or drifting insects than their wild counterparts. These dietary differences have also been observed in the Salmon River (New York) by Johnson (1981), where the diet of wild and hatchery reared yearling rainbow trout did not significantly overlap. Petrosky (1985) demonstrated that stocking rainbow trout at low densities (50-100 fish/stream section) did not affect the abundance, dispersal, mortality rate, growth rate, or condition factor of wild rainbow trout. However, at high densities (400 fish/section) the mortality rate of wild fish was significantly increased.

Leider et al. (1984) investigated the reproductive activity of wild and hatchery reared winter and summer run steelhead trout placed in enclosures. There was some temporal segregation of spawning with hatchery summer steelhead (average date, January 10) spawning before wild summer steelhead (average date, February 15), which spawn before hatchery winter steelhead (average date, March 6), that in turn spawn before wild winter steelhead (average date, April 14). For both hatchery and wild summer steelhead the selection of spawning sites was randomly distributed throughout the enclosures. In contrast, wild winter steelhead primarily spawned in the lower sections of the enclosures. Although there was some overlap, most interactions occurred among members of the same spawning group. Wild winter and hatchery summer steelhead were the most reproductively discrete spawning groups, having 95.1 and 93 % intra-group spawning activity, respectively. Reproductive exchange was greatest for hatchery winter steelhead, with only 36.7% intra-group crosses; and intermediate for wild summer steelhead, with only 63.9% intra-group crosses. Complete reproductive isolation was not observed between wild and hatchery steelhead in Gober Creek. This suggested that, although temporal segregation may reduce spawning between wild and hatchery reared steelhead trout, spatial separation was also required to eliminate interbreeding and reproductive competition.

As with chinook salmon, intra-specific competition between wild and hatchery reared steelhead-rainbow trout will probably occur whenever they share the same microhabitat and dietary needs. This is a function of both when, where, and how the hatchery fish are released, as well as the microhabitat and dietary preferences shown by the two rearing types. The less hatchery fish share the habitat and dietary requirements of wild fish the less likely the two forms are to compete. Thus the release of steelhead trout fry or pre-smolts into habitat with resident wild steelhead-rainbow has great potential for producing competition between the two rearing types. In contrast, the release of well imprinted and rapidly migrating steelhead trout smolts from hatcheries which are geographically separated from wild fish rearing and spawning areas may generate very little competition between wild and hatchery reared steelhead-rainbow trout.

A summary of the studies on intra-specific competition between wild and hatchery-reared steelhead trout is given in Table 7.

Table 7. Studies observing possible competition between wild and hatchery reared steelhead trout.



Study	Stage	Freshwater rearing	Migration corridor	Estuary	Ocean	Adult migration	Spawning
Allee 1974	fry	neg					
Bjornn 1978	fry	neg					
Berejikian 1995a	fry	neg					
Johnson 1981	yearlings	none					
Vincent 19??	catchable	neg					
Pollard 1969	catchable	0-neg					
Petrosky 1985	catchable	0-neg					
Leider et al. 1984	spawners	0-neg					
Gut feeling using good hatchery rearing and release protocols	smolts	none	none	minor	minor	none	none

Competition between steelhead trout and chinook salmon

In theory, inter-specific competition between age-0 steelhead trout, age-1 steelhead trout, and age-0 spring chinook salmon is minimized by each age-species class occupying different spring-summer microhabitats. The diet and microhabitat requirements of the two species are very similar, with fish of both species moving into faster more food rich waters as they grow. This progressive movement of juveniles into higher velocity water, coupled with different species-specific emergence times, minimizes inter-specific competition between the two species. Everest (1969) observed that earlier emerging and larger spring chinook fry generally moved into faster water habitat before the smaller age-0 steelhead trout fry emerged. Similarly, the larger age-1 steelhead trout parr primarily occupied faster water than age-0 spring chinook salmon.

In field studies both within and outside the Snake River Basin over a long period (Everest 1969, Chapman and Bjornn 1969, Everest and Chapman 1972, Hillman et al. 1989, Roper et al. 1994), spring chinook salmon fry were shown to occupy primarily different spring-summer microhabitat than either 0-age or I-age steelhead-rainbow trout. However, there was usually some minor overlap (about 10-20%) in microhabitat use between the two species. This overlap suggested that the in-stream distribution of the two species was probably the product of either the size-microhabitat theory discussed above or displacement from inter-specific aggression.

The microhabitat differences between steelhead trout and spring chinook salmon fry have also been observed outside the Columbia River Basin. Roper et al. (1994) observed that steelhead trout used every type of habitat in the study stream, while juvenile spring chinook were heavily concentrated in pool habitats. This led the authors to conclude that the two species were primarily utilizing different summer habitats. This habitat separation should act to minimize inter-specific competition.

Some inter-specific aggression was observed between steelhead trout and spring chinook salmon fry in Snake River tributaries by Everest (1969). However, similar inter-specific aggression between the two species was not observed in Wenatchee River system, even though intra-specific aggression among spring chinook salmon fry was observed by Hillman et al. (1989a, 1989b). Everest (1969) found that removal of steelhead trout from sections of Idaho streams resulted in shifting the distribution of spring chinook salmon. Although he concluded that inter-specific competition between steelhead trout and spring chinook salmon did not exist, his observation of inter-specific aggression between the two species, and finding that spring chinook salmon fry shifted their habitat distribution when steelhead were removed, raises the possibility that some level of inter-specific competition between the two species exists.

Bjornn (1978) observed that, between 1963 to 1967, the production of spring chinook salmon from Big Springs Creek, a tributary of Lemhi River, declined coincidentally with the planting of 0-age steelhead trout. When hatchery spring chinook salmon were later planted in the system steelhead trout production was similarly reduced. Although he explained the reduction of spring chinook salmon fry as a function of adult seeding, inter-specific competition between the wild-produced spring chinook salmon fry and the planted hatchery trout fry might have occurred. When 0-age hatchery produced steelhead trout fry were released into the Wenatchee River system, no similar negative impact was observed by Hillman and Mullan (1989) on wild-produced spring chinook salmon fry. Although suggestive of inter-specific competition between the two species, these results do not conclusively prove that it does or does not occur.

The interaction between chinook salmon and steelhead trout in the Yakima River system has been studied by McMichael et al. (1997) in relation to a proposed supplementation program. They found little evidence of competition between steelhead trout and chinook salmon. The residual steelhead trout from releases of hatchery reared fish did not adversely effect the growth of wild spring chinook salmon, even when the trout were nearly twice as large as the salmon. Similarly, McMichael and Pearson (1998) found that the growth of steelhead-rainbow trout in small cages and enclosures was not negatively impacted by the presence of spring chinook salmon parr. Observations by scuba divers during the course of this study indicated that spring chinook salmon held higher in the water column and over deeper water than steelhead-rainbow trout.

Bjornn (1978) observed that most spring chinook salmon migrated in the fall from their spring-summer rearing tributaries into the main stem of the Lemhi river where they over-wintered and out-migrated as smolts the following fall. Everest (1969) and Hillman et al. (1989a, 1989b) found that both steelhead-rainbow trout and spring chinook salmon ceased to feed in winter and hibernated in low velocity interstices in the substrate. This might suppose that there is no inter-specific competition in this critical over-winter microhabitat, but carefully designed and well controlled experiments with allopatric and sympatric populations will be required to determine if this is the case. Any such study should also include research on inter-specific aggression and habitat displacement.

When migrating to sea as smolts in the mid-Columbia River it appears that both yearling spring chinook salmon and steelhead trout migrate downstream in the main channel away from the shore. Dauble et al. (1989) recovered steelhead out-migrants primarily between mid-water and the bottom. Although this migration pattern separates the two from juvenile fall chinook salmon habitat, it places them in similar migration corridor habitat allowing for the possibility of inter-specific competition.

Finally, Everest (1969) pointed out that, although steelhead and chinook may spawn in the same areas in streams, the timing of spawning was such that incubation and emergence of each species was completed before spawning areas were again utilized. Thus inter-specific competition for spawning sites should be negligible.

A summary of the studies on intra-specific competition between steelhead trout and spring chinook salmon is given in Table 8.

Table 8. Studies observing possible competition between steelhead trout and spring chinook salmon.

Study	Stage	Freshwater rearing	Migration corridor	Estuary	Ocean	Adult migration	Spawning
Everest 1969	fry	none-neg					
Hillman et al. 1989a, 1989b	fry	none					
Roper et al. 1994	fry	none-neg					
Bjornn 1978	fry	neg					
Hillman and Mullan 1989	fry	none					
McMichael and Pearson 1998	fry	none					
McMichael et al. 1997	residual	none					
Dauble et al. 1989	smolt		unk-none				
Everest 1969	spawner						none
Gut feeling using good hatchery rearing and release protocols	smolt	none	none	none	none	none	none

Hatchery practices for minimizing competition

For a number of years new and improved strategies for minimizing the occurrence of competition between wild and hatchery reared salmonids have been developed. Generally these strategies involve reducing the habitat and diet overlap between the two rearing types. Releasing hatchery salmonids as true smolts which rapidly migrate downstream to the estuary and marine environment minimizes or eliminates competition with wild fish rearing in streams, rivers, and lakes. By ensuring these fish are properly imprinted and can return to their natal hatchery, fish managers can minimize the opportunity for them to compete with wild reared salmonids for rearing sites. The possibility of competition can be further reduced by locating hatcheries away from natural spawning areas.

Managers can also consider increasing the spatial and temporal separation between hatchery and wild fish by releasing hatchery fish so that they remain spatially and temporally separated from wild salmon in estuarine and oceanic habitat. Suggested approaches include producing large fish which do not utilize the same microhabitat as smaller wild salmonids, releasing hatchery fish after wild salmonids have moved out of estuarine habitats, and releasing hatchery fish in habitat downstream of that used by wild-reared salmonids. Manager might also consider the intentional development of salmonid strains with different temporal (migration and reproductive timing), spatial (microhabitat use), and dietary requirements than wild reared salmon to reduce the potential for competition between the two stocks.

C. Predation

Introduction

The effects of artificial propagation on predator prey-interactions involving ESA-listed salmonid populations can be divided into three major categories. First, salmon released from hatcheries might prey on wild fish. Second, releases of hatchery fish may influence the behavior and dynamics of predator populations, which can indirectly affect wild fish. Third, hatchery rearing and release protocols can influence the vulnerability of hatchery-reared salmonids (cultured for conservation purposes) to predators after release. This review focuses on predator-prey interactions of anadromous Pacific salmon and, where information is available, focuses on chinook salmon and steelhead in the Columbia/Snake River system.

Predation by hatchery-reared steelhead and chinook salmon on wild steelhead and/or chinook salmon

Five separate studies investigated predation by hatchery released steelhead on wild chinook salmon in Columbia and Snake River tributaries. Predation by hatchery steelhead and hatchery chinook on wild chinook was reported in two additional studies in Northern California by Menchen (1981) and Sholes and Hallock (1979), and one in British Columbia by Levings and Lauzier (1989). Details are discussed in the following paragraphs.

Whitesell et al. (1993) and Jonasson et al. (1994, 1995) found a very low incidence of residual steelhead predation on wild chinook salmon juveniles. In fact in two of the three years they found no evidence of predation in stomach samples of 368 and 641 residual steelhead. These studies did not attempt to estimate predator or prey abundance, and made simple estimates of consumption rates without error estimates.

Martin et al. (1993) estimated that a total of 456 chinook juveniles were eaten by residual steelhead over a 6 month period in the Tucannon River and Asotin Creek, both tributaries of the Snake River. They did not estimate prey abundance and therefore it was impossible to estimate the proportion of the chinook population consumed.

Cannamella (1993) provided perhaps the most complete investigation of hatchery steelhead predation on wild chinook salmon. The study reported predator abundance, estimated consumption per predator (based on empirically derived gastric evacuation rates), and estimated prey abundance. Based on data provided in the report, an estimated 4.8% to 21.7% (95% C.I.) of naturally spawned chinook fry were consumed by steelhead during the 50 days following the release of 744,000 steelhead smolts. However, this probably underestimated the total predation impact, because estimates were not expanded to include possible predation by residual steelhead predation beyond June 3, and the study was conducted in a year in which prey abundance was low.

Two reports from Northern California indicated much higher levels of predation by age-1 hatchery chinook salmon (Sholes and Hallock 1979) and steelhead (Menchen 1981) on wild chinook salmon than have been reported in the Columbia/Snake River system. However, neither of these studies estimated prey abundance, nor did they estimate error associated with the reported predation rates.

There was no documentation of predation by hatchery-released salmon or steelhead on wild steelhead fry, although some of the ‘unidentified salmonids’ reported in these studies may have been steelhead.

The US Fish and Wildlife Service (USFWS 1992) summarized existing information for the Columbia/Snake River system. The study concluded that the number of fry/fingerlings eaten by hatchery-produced steelhead was, “…low or negligible, either because of low rates of predation, the lack of coexistence, or both; and too many assumptions would have to be made to confidently estimate the actual number of chinook salmon fry and fingerlings consumed (or to calculate their resulting adult equivalents).” Information summarized since the completion of that report, by Whitesell et al. 1993, and Jonasson et al. 1994, 1995) supported their conclusions.

In conclusion, existing evidence suggests that hatchery-released steelhead and chinook salmon will consume wild chinook salmon juveniles, and possibly steelhead juveniles in the Columbia/Snake River system. The range of impact on the prey populations may range from 0% to greater than 22% in tributaries of the Columbia and Snake Rivers.

Effects of hatchery releases on the behavior and dynamics of predator populations, and indirect impacts on wild salmonids

Predator attraction – Northern pikeminnows are the primary predator on juvenile salmon in the Columbia River Basin, according to Reimen et al. (1991). Predation by northern pikeminnows on juvenile salmonids has generally been reported to be higher near hatchery release sites (Ledgerwood et al. 1993, Collis et al. 1995) than away from release sites (Buchanan et al. 1981, Poe et al. 1991, Ward et al. 1995). However, Shively et al. (1996) demonstrated that northern pikeminnows quickly exploited hatchery-released spring chinook salmon approximately 60 km away from their release site. In that study, northern pikeminnow diets consisted of 0% salmonids one day prior to the release of 1.1 million spring chinook salmon. Eight days after their release, spring chinook salmon were found in 86% of northern pikeminnows sampled.

Following three large-scale hatchery releases of spring chinook salmon into tributaries of the Bonneville Pool, Collis et al. (1995) found that the abundance of northern pikeminnows near hatchery release sites increased rapidly (within a day or so), and their diet shifted from exclusively non-salmonids to a predominantly salmonid diet. Thus, hatchery releases can attract predators to areas near hatchery release sites in the Columbia River Basin, and northern pikeminnows can quickly exploit hatchery-released chinook salmon.

The rapid numerical response (predator abundance) and functional response (number of prey eaten per predator per unit time) to large-scale hatchery releases could have either a positive or negative impact on wild fish. For example, concentrating predators near hatcheries could expose wild fish in those areas to greater predation pressure posed by significantly increased numbers of predators. On the other hand, predators migrating towards large numbers of hatchery fish concentrated near release sites would reduce their numbers in other areas of the migratory corridor, which may reduce predation on wild fish in those areas. There was no evidence that increased predator abundance or increased predation rates on recently released hatchery salmon either increased or decreased predation on wild salmonids near or away from hatchery release locations.

Predation buffer – Theoretically, predation on wild fish may be reduced if the numbers of hatchery-produced fish released exceeds the capacity of the predator population to consume the additional prey. Studies by Peterman and Gatto (1978), Ruggerone and Rogers (1984), Fresh and Schroder (1987), and Peterson and De Angelis (1992) investigated the ‘functional response’ (i.e., number of prey eaten per unit time per predator) of predators to salmonid prey. In the Columbia River, Petersen and De Angelis (1992) found that northern pikeminnow predation on juvenile salmon below McNary Dam fitted a type II or type III functional response. Both of these curves have an upper limit (asymptote) to the predation rate by a predator population. Numerous factors can affect the functional response relationships, according to Ruggerone and Rogers (1984). Generally, however, as prey abundance increased above a given level (the asymptote), predation was depensatory.

The presence of large numbers of hatchery fish could reduce predation on wild fish under such conditions only if the abundance of local predator population remained stable or decreased. Collis et al. (1995) believed this would probably be a false assumption in the Columbia River. Thus, without complimentary information on both the functional and numerical response of predators to prey, predictions as to how increases or decreases in hatchery fish abundance will affect predation on intermixed wild fish would be unfounded. In short, there is no information which suggests that increased or decreased abundance of hatchery-produced salmon affects predation on intermixed wild salmonids.

Long-term increase in predator populations – Increases in predator populations caused by long-term hatchery production are likely to increase predation on wild fish. Kirn et al. (1986) and Beamesderfer and Rieman (1991) demonstrated that Northern pikeminnow abundance in the Lower Columbia River appeared to increase during the 1980s at the same time that hatchery releases increased quite markedly. However, no causal relationship between increases in the number of hatchery-released fish and long-term increases in population abundance of northern pikeminnows, or any other predator, has been established.

In conclusion, releases of hatchery-reared fish do affect the behavior of predator populations in the Columbia River system, however, no studies have demonstrated the effects of such changes on intermixed wild populations. The effects could be either positive or negative for wild populations.

Effects of hatchery rearing and release strategies on vulnerability of cultured salmonids to predation.

(a) Rearing strategies

Color acclimation – Semi-natural rearing techniques have been implemented to improve the cryptic coloration of salmonids and improve their post-release survival. Improved survival of fish from rearing tanks containing gravel substrates has been attributed by Maynard et al. (1995 and 1996a) to greater cryptic coloration and consequent improvement in predator avoidance. However, numerous potential behavioral or physiological attributes may have contributed to the increases in post-release survival, and the reported differences in coloration were not directly attributed to predation.

Color acclimation has been shown to reduce vulnerability to hooded mergansers in laboratory raceways in some situations, but not all (Donnelly and Whoriskey 1991, 1993). Atlantic salmon acclimated to tan colored substrates exhibited a 5:1 survival advantage over brown-acclimated salmon when both were exposed to mergansers in tan colored raceways. However, in brown raceways, the color-acclimated brown fish exhibited a 0.5:1 survival disadvantage. Color-acclimated brook trout survived at a higher rate in tan (1.9:1 survival) and brown raceways (1.5:1).

Anti-predator conditioning – Anti-predator conditioning efforts have involved various combinations of visual, olfactory, and auditory stimuli, all of which can trigger innate anti-predator responses. Conditioning, using a combination of injured conspecific predator odors in the absence of visual and auditory stimuli, has been found to improve subsequent predator recognition and avoidance behavior in rainbow trout and chinook salmon.

A few studies have demonstrated an increase in post-release survival of juvenile salmonids following anti-predator conditioning in hatchery vessels. Both Thompson (1966) and Kanayama (1968) demonstrated that post-release survival of chinook and chum salmon smolts exposed to electrified predator models was greater than for non-conditioned smolts. Berejikian et al. (1999) found that chemical anti-predator conditioning of chinook salmon smolts in hatchery tanks containing complex structures improved their post-release survival in a natural stream, but conditioning did not improve the survival of smolts reared in barren vessels. There is as yet no evidence that anti-predator conditioning reduces post-release survival.

Fish health – Bacterial kidney disease (BKD) is a major pathogen of fish in hatcheries of the Pacific Northwest, including the Snake and Columbia River Basins. Mesa et al. (1998) found a significant effect of Rs infection on the ability of juvenile chinook salmon to avoid predation by northern pikeminnows and smallmouth bass in experimental raceways. Infected fish were eaten by about twice as frequently as non-infected fish by northern pikeminnows (1.98 infected: 1 control) and smallmouth bass (1.94 infected: 1 control). Measures to control the incidence of BKD in hatcheries culturing ESA-listed stocks, and in natural streams, should decrease predation mortality.

In summary, rearing strategies might be modified to reduce the vulnerability of cultured salmonids to predators. The effects of the different strategies outlined above are probably not additive. The benefits may range from the high of 50% decrease in predation related mortality (described by Mesa 1998) to the low of 0% (reported by Berejikian et al. 1999).

Acclimating the color of fish in rearing vessels to that of post-release environment may offer some reduction in their vulnerability to predators. However, techniques may probably have to be developed for each rearing and release location, and perhaps for each species.

(b) Release strategies

Time of day - Ruggerone (1986) found that the number of salmonids consumed by gulls in the Columbia River declined from approximately 400 fish per hour to nearly 0 fish per hour between 1800 and 2030 hrs. Decreased light intensity also reduced predation by rainbow trout on sockeye salmon fry (Ginetz and Larkin 1976). Patten (1977) found that torrent sculpin consumed greater numbers of coho salmon fry (70% mortality) on moonlight nights compared with darker nights (24% mortality) in laboratory aquaria. Predation by sculpin was not a significant factor for salmon larger than ~60 mm, and therefore would only apply to programs releasing age-0 juveniles.

Ginetz and Larkin (1976) found that predation by rainbow trout on sockeye salmon fry increased as light intensity decreased from .30 ft-c to 0.05 ft-c, but predation decreased as light intensity further decreased to 0.01 ft-c (simulated cloudy skies and moonlight nights). Predation on salmonids appears to decrease at very low light levels, so releasing salmon at night may reduce predation on them during the first several hours after release. Fish are presumed to be at greatest risk of predation during the first hours to days following release, due to handling stress and lack of experience in recognizing and avoiding predators.

Release method and abundance – The rate of predation on juvenile salmon will partly depend on, among numerous other factors, the abundance of the prey and predator populations. The issue for hatcheries is whether to release smaller numbers of fish over a protracted time period (e.g., volitional release) or large number in a single ‘pulse’.

Fresh et al. (1980) found that freshwater survival of chum salmon released from a hatchery increased from 40.3% to 91.5% as the numbers of salmon released increased from 517 fry to 50,155 fry. In a later study, Fresh and Schroder (1987) demonstrated concomitant mortality for release numbers of chum salmon ranging between 50 and 1,200 fry. Wood (1987) determined that predation by common mergansers on migrating salmonids (including chum, coho, chinook, and steelhead) was depensatory during the period of seaward migration in Vancouver Island, BC streams. He suggested that predation rates on hatchery released salmon would be reduced by releasing large numbers of smolts over a short time period. Other studies by Neave (1953) on chum and pink salmon, Hunter (1959) with pink, and McIntyre and Wilmot (1988) with sockeye, have all demonstrated depensatory mortality in natural predator-prey systems. However, no studies have directly investigated the effects of release number and duration on predation of chinook salmon and steelhead.

In summary, release strategies for large numbers of hatchery reared chinook salmon and steelhead at night should decrease overall predation. The level of predation will depend on numerous environmental factors as well as characteristics and abundance the predator populations.

Table 9, which follows, summarizes known data for predator-prey interactions between wild and hatchery-reared salmonids in the Pacific Northwest.

D. Fish Health

Introduction

Infectious diseases are an integral part of the existence of all animals, including both cultured and wild fish populations. Hedrick (1998) summarized the many perceptions and misperceptions held by the public and scientific community regarding the spread of infectious disease from cultured or hatchery raised fish to wild fish. While it is true that human activities have affected fish health through direct changes in habitat and ecosystems, these changes do not necessarily mean that fish pathogens were, or are, actively introduced through these actions.

With the exception of the unintentional introduction of ‘exotic’ pathogens in an ecosytem, fisheries pathologists indicate that most if not all pathogenic microorganisms existed in wild fish populations before the introduction of hatcheries (Sinderman 1990, Kent et al. 1998, Whittington et al. 1997). While hatchery populations can be considered reservoirs of infectious agents because of exposure to higher rearing densities and stress, according to Saunders (1991), Hastein and Lindstad (1991) said there was little evidence to suggest that disease transmission to wild stocks is routine. Therefore, it is extremely difficult to determine the incidence of disease transmission from hatchery to wild fish, as well as the impacts such transmission would have on wild stocks.

Specific determination of the origin of any particular pathogen found in a wild fish requires the ability to distinguish different strains of a pathogen at the genetic level. While such epidemiological tracking can be done on all classes of infectious pathogens (i.e., bacterial, viral, parasitic, and fungal) using a variety of molecular methods, these techniques have not been applied to many salmonid pathogens. In many cases reliable genetic strain markers have not been available, such as with *Renibacterium salmoninarum* the causal agent of bacterial kidney disease. However, recent advances reported by Grayson et al. (1999) in genetics and molecular biology may make this feasible in the near future.

Table 9. Predator prey interactions between hatchery-reared and naturally produced (wild) salmonids along the Pacific Coast of North America.

River	Interaction[1]	Duration	Prey/predator (n)	Estimate error	Predator abundance (n)	Predators sampled (n)	Prey abundance (n estim.)	Estimated consumption of prey population	Citation
Upper Salmon (ID)	Hsthd –Nchin	50 days Apr. - May	1.5×10^{-3} / predator/day	5.5×10^{-4}-2.4×10^{-3} (95% C.I.)	744,000 released	651	184,000 fry	4.9-21.7% (95% C. I.)	Cannamella (1993)
N/A	Hsthd-Nchin	Apr. – Aug.	4.5×10^{-3}/ stom.	N/A	N/A	222	N/A	N/A	Partridge (1986) in USFWS (1992)
Tucannon & Asotin (WA)	Hrsthd-chin	4/14-10/31	1.6×10^{-3}/ stomach	N/A	129,070 released	1894	N/A	456	Martin et al. (1993)
Gr. Ronde & Imnaha (OR)	Hrsthd-Nchin	Win. Spr. Sum. & Aut.	0/stomach	N/A	N/A	611	N/A	N/A	Whitesell et al. (1993)
Gr. Ronde & Imnaha (OR)	Hrsthd-Nchin	Win. Spr. Sum. & Aut.	0/stomach	N/A	N/A	368	N/A	N/A	Jonasson et al. (1994)
Gr. Ronde & Imnaha (OR)	Hrsthd-Nchin	Win. Spr. Sum. & Aut.	5.7×10^{-3} /stomach	6.0×10^{-4} - 2.9×10^{-2} /stom. (95% C.I)	N/A	175	N/A	N/A	Jonasson et al. (1995)
Battle Cr. (CA)	Hsthd –Nchin	2/20-4/18	1.24/stomach		653,317 released	910	8.3 million eggs dep.	NA	Menchen (1975)
Feather (CA)	Hchin (1+) – Nchin	1/1-2/28	1.30/stomach	N/A	532,000 released	N/A	N/A	7.5 million (max)	Sholes and Hallock (1979)
Nicola (BC)	Hchin – Nchin	In smolt migration	0/stomach	N/A	291,150	382	N/A	N/A	Levings and Lauzier (1989)
Rogue (OR)	Chin, Rsthd, & Coho on salmonid fry	3/1-6/1 over 3 yr.	See Table 33 in report	N/A	N/A	N/A	N/A	N/A	Evanson et al. 1981
Cedar (WA)	Wsthd – Nsoc	1-120 d/yr. over 3 yr.	N/A	N/A	12,200 to 28,700	89	45 million fry	1.4-21.2 m. or 3.1-47.7%	Beauchamp (1995)
Cedar R.	Hsthd – Nsock	1-120 d/yr. over 3 yr.	N/A	N/A	36,225	13	N/A	N/A	Beauchamp (1995)

[1] The interaction is listed as predator – prey, using the following abbreviations:
H = hatchery; N = natural; sthd = steelhead; rsthd = residual steelhead; chin = chinook; soc = sockeye.

In 1984, the Pacific Northwest Fish Health Protection Committee[1] (PNFHPC) established policies designed to prevent the spread of pathogens that might result in the release of seriously infected salmon from hatcheries. This policy calls for destruction of fish infected with the most serious pathogens. These policies were updated in 1989 by the PNFHPC[2] followed by the establishment of the Salmonid Disease Control Policy of the Fisheries Co-Managers in 1992. It is suggested that any supplementation project be conducted in a manner that is consistent with these guidelines, which define rearing, sanitation, and fish health practices that minimize the incidence of disease outbreaks in propagated populations. For example, cultured salmon should never be released that are infected with any of the virulent salmonid viruses, such as IHNV. However, because of limitations in diagnostic procedures for many pathogens, it is difficult to assure that any hatchery fish are 100% free of pathogens. In many cases this would also be impractical, since as discussed previously, these same pathogens may be present in wild stocks as well.

Important salmonid pathogens

The available scientific literature on the spread of infectious disease between hatchery and wild populations of fish is somewhat limited. According to the PNFHPC guidelines, the eight most important diseases of salmonids which should be part of fish health screens prior to release from Pacific Northwest hatcheries are:

bacterial
- Bacterial kidney disease (BKD), caused by *Renibacterium salmoninarum*
- Bacterial coldwater disease (BCD), caused by *Flexibacter psychrophilus*

viral
- Infectious hematopoietic necrosis virus (IHNV)
- Erythrocytic inclusion body syndrome (EIBS), probably viral etiology

fungal
- miscellaneous species

parasitic
- Ceratomyxosis, caused by *Ceratomyxa shasta*
- Whirling disease, caused by *Myxobolus cerebralis*
- Gill and skin parasites *Ichtyoptherius* spp. and *Ichtyobodo* spp.

In addition to this list, infectious pancreatic necrosis virus (IPNV) and viral hemorrhagic necrosis virus (VHSV) are included in routine health screens. IPNV is readily shed by infected fish and thus they should not be released. However, the significance of VHSV infection in

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[1] The PNFHPC includes administrative and fish pathologist representatives from the Washington Department of Fish and Wildlife, Oregon Department of Fish and Wildlife, California Department of Fish and Wildlife, Idaho Department of Fish and Game, Alaska Department of Fish and Wildlife, U.S. Fish and Wildlife Service, National Marine Fisheries Service (Northwest Region), Northwest Indian Fish Commission, and other private parties representing aquaculture interests.

[2] Model comprehensive fish health protection program, Pacific Northwest Fish Health Protection Committee, 1989, 19 p.

Pacific Northwest salmon is less clear. According to Kocan et al. (1997), the strain endemic to the area appears to be highly pathogenic for Pacific herring but significantly less pathogenic to salmonids than the European strain. Therefore, routine screening and isolation of VHSV should be followed up by strain determination after Basurco et al. (1995).

There is no specific information pertaining to contraction of any of these infectious diseases from interactions with hatchery stocks in the Upper Columbia River steelhead and Snake River spring/summer chinook Evolutionarily Significant Units (ESUs). Therefore, this review will serve to present an overview of selected data on spread of infectious disease in and between fish populations, with an eye towards interpreting the studies as to how they may relate to cultured and wild salmonids. It will focus on three areas, namely, the spread of infectious agents (i) from cultured to wild stocks, (ii) from wild to cultured stocks, and (iii) through other vectors.

The spread of infectious agents from hatchery fish to wild stocks

BKD - *R. salmoninarum* can be found world wide in both *Salmo* and *Oncorhynchus* genera. Improvements in detection sensitivity has shown that the bacterium is present in most, if not all, salmonid populations in the Pacific Northwest. Depending on the technique used to detect *R. salmoninarum*, the percentage of fish infected in hatcheries can range from 10-100%, although no disease symptoms are present (Rhodes et al. 1998). Using the enzyme-linked immuno-adsorbent assay (ELISA), surveys of hatchery and wild spring-summer chinook collected at various dams during out migration on the Snake and Columbia rivers by Elliott et al. (1997) showed that 68-87% of the fish were infected, although only 1-11% of fish at any one site showed symptoms of BKD.

There is little data available to help determine the chance of survival of infected fish to maturity, although hatchery fish from broodstock with low *R. salmoninarum* levels have a significantly increased chance of survival in seawater over the progeny of those with high *R. salmoninarum* levels (Elliot et al. 1995). Stress is prime activator of quiescent *R. salmoninarum* infections, and this includes the transition to saltwater and possibly during the crowding of fish in transportation barges. Therefore it is possible that heavily infected hatchery fish could transmit disease to wild stocks because of bacterial shedding that occurs in active *R. salmoninarum* infections. However, this has not been shown directly.

Transmission of disease to wild trout from infected hatchery trout has been demonstrated by Mitchum et al. (1979). Mitchum and Sherman (1981) also showed that wild trout could transmit the disease to hatchery fish in small lake and stream systems. This may have some bearing for the horizontal transmission of the bacterium between either juvenile fish after release in stream systems or during spawning.

In general, horizontal transmission of *R. salmoninarum* results from fecal shedding of bacteria by infected fish. Once shed, the bacteria can survive up to 21 days in feces or sediment under freshwater conditions (Austin and Rayment 1985) and at least 2 weeks in filter-sterilized seawater (Balfry et al. 1996). A fecal-oral route of transmission is implicated in horizontal transfer in farmed salmon (Balfry et al. 1996) but infection through other epithelia such as skin or gill may also occur (Flano et al. 1996). This is an important point to consider when trying to assess the transmissibility of any infectious agent from hatchery to wild fish, and emphasizes the prudence of thorough health screens on hatchery fish prior to release.

Furunculosis - *Aeromonas salmonicida*, the causal agent, is endemic in salmonids world wide. The most significant outbreaks of disease occur in farmed Atlantic salmon or rainbow trout. The disease usually occurs only under conditions of overcrowding or stress. Furunculosis has been epidemic in some Norwegian fish farms since 1985, possibly after an initial introduction from the importation of latent infected Atlantic salmon smolts from Scotland. It has been hypothesized by Hastein and Lindstad (1991) that the disease spread to fish in 20 Norwegian rivers from escaped fish, but the significance on overall wild fish survival is unknown..

Parasitic lesions - *Gyrodactylus salaris* is a parasite of Atlantic salmon which causes extensive lesions over the body of infected fish. High infestations have been a significant cause of mortality in Norwegian hatcheries and fish farms. Johnsen and Jensen (1986) found some evidence that *Gyrodactylus* was introduced into the wild populations in several Norwegian rivers from the release of infected hatchery fish, which in turn had become infected from fish imported into the hatcheries from elsewhere in Scandinavia.. Recently, Soleng et al. (1998) demonstrated that Atlantic salmon smolts could transmit the parasite to parr, and that adult salmon can serve as reservoirs of the parasite.

Whirling disease - There are numerous publications on the spread of *Myxobolus cerebralis* in the trout population, but little on the effects of the parasite in salmon. Chinook salmon and steelhead are sensitive to infection with *M. cerebralis* and show typical disease if exposed at a young age, while coho are resistant to disease even though they can be infected (Ronald P. Hedrick, pers. commun.). To date there is no evidence available about the effect of whirling disease on anadromous salmon populations.

Spread of infectious agents from wild fish to hatchery stocks

IHNV - Meyers (1998) recently reported that juvenile sockeye salmon in Alaska reared in virus-free hatchery water returned as IHNV-infected adults. The virus was isolated in high titers from fish that matured in either fresh or salt water. However, as the author pointed out, it is difficult to determine whether the source of virus was a reservoir in either fresh or seawater (possibly from non-salmonid fish species), or whether there was vertical transmission from parents with subclinical, undetectable infections. The report illustrates the difficulty in eliminating a pathogen from anadromous fish populations.

Similar IHNV infections in returning chum and chinook salmon at an Alaskan hatchery were noted by Follett et al. (1987). They raised the possibility that horizontal transmission of the virus could have come from resident kokanee in the hatchery water supply.

BKD - Natural horizontal transmission of *R. salmoninarum* and subsequent development of BKD was demonstrated by Mitchum and Sherman (1981) by exposing hatchery-raised brook, brown, and rainbow trout to naturally infected brook trout kept in a small lake and stream system. This study showed that *R. salmoninarum* is transmissible from fish to fish outside of a hatchery setting. Previously, Mitchum et al. (1979) had demonstrated that infections of wild trout could originate with hatchery fish as well.

Bacterial pathogens - *Streptococcus iniae* is a bacterial pathogen capable of causing infections in salmonids, tilapines, and many other fish species. Zlotkin et al. (1998) isolated the pathogen from diseased wild fish near marine fish culture facilities where gilthead sea bream and European sea bass exhibited similar infections. Bacterial species-specific PCR and ribotyping confirmed that the wild and cultured fish were infected by a single *S. iniae* clone, suggesting that the wild fish are potential amplifiers of pathogenic bacteria.

Spread of infectious agents through other vectors

There have been numerous reports of transmission of infectious agents from fish to other fish via passage through an intermediate host. The most famous example is the organism responsible for whirling disease, *M. cerebralis,* that is passed from fish to fish through oligochaete worms, *Tubifex tubifex* (Rognlie and Knapp 1998). However, birds appear to be able to spread pathogens as well through their feces, after ingestion of infected fish. This has been clearly shown for a number of salmonid and other fish pathogens, including IHNV and VHSV by Peters and Neukirch (1986), epizootic haematopoietic necrosis virus (EHNV) in redfin perch by Whittington et al. (1996), and *M. cerebralis* by Taylor and Lott (1978). Recent media reports (Seattle Times, Jan. 17, 1998; Seattle Post-Intelligence, May 24, 1999) of Caspian terns eating out-migrating juvenile salmon in the Columbia river suggest that these birds could serve as a reservoir for infectious disease agents and subsequently transfer them to other wild fish populations through their feces.

E. Migratory Behavior

Potential migratory behavioral interaction between hatchery and wild fish includes a downstream schooling influence. This refers to the downstream sweeping of wild fish by large numbers of downstream migrant hatchery fish, known commonly as the ‘pied piper effect.’ The phenomenon has been observed and reported by scuba divers. Despite these reports, there is little or no documentation of the frequency of the phenomenon, or the conditions under which it occurs. There are no quantitative studies of the impacts of such behavior on subsequent survival of Pacific salmon species, or data documenting the effects on differential survival between hatchery and wild fish.

There are some reports of sweeping phenomena occurring during the out-migration of young Atlantic salmon. Hansen and Jonsson (1985) observed that stocking receiving waters with hatchery-reared smolts seemed to initiate formation of schools during the period of smolt out-migration. This school formation phenomenon is not absolute, as the simultaneous release of two different stocks of juvenile Atlantic salmon showed that only some of one stock followed the more rapidly migrating stock downstream, but the majority of the slower stock remained behind (Aarestrup et al. 1999). Clearer documentation of the schooling phenomenon has been provided by Hvidsten et al. (1995), who showed that the time to travel to a downstream trap was independent of the distance from the point of release when the fish were traveling in schools.

There is no clear published evidence of the impact of downstream sweeping of smolts on subsequent survival. Hvidsten and Johnsen (1993) suggested that such a phenomenon may result in increased smolt-to-adult survival (SAR). They recorded 6.8% SAR for hatchery-reared Atlantic salmon released into a stream during peaks of smolt out-migration compared with only 2.6% SAR during the troughs.

IV. CONCLUSIONS AND RECOMMENDATIONS

The recent listings of Northwest salmon stocks as threatened or endangered under the ESA has initiated renewed focus on the operation of the public fish hatchery system in the Pacific Northwest. Hatchery strategies offer the potential to stabilize and amplify salmonid populations. Nonetheless, it is clear that the artificial culture environment conditions salmonids to respond to food, habitat, con-specifics, and predators in ways different from those of fish reared in natural environments. Consequently, fundamental changes in the dynamics of hatchery production policy and implementation may be necessary both where hatchery supplementation is used to maintain some populations until underlying causes of decline are corrected, and where production hatchery operations overlap listed stocks.

Potential effects of artificial production strategies on population dynamics of wild salmon is a primary concern for ESA-listed stocks. Tables 10 and 11 summarize an assessment of the potential effects of artificial production strategies on population abundance of wild Snake River spring/summer chinook and Upper Columbia River steelhead in their respective ESUs. Unfortunately, the overall effectiveness of supplementation to maintain a population until underlying causes of decline are corrected is unknown. Very little specific numerical information exists regarding population abundance dynamics or interactive factors, such as competition, predation, migration, and fish health. Therefore, for the most part, the assessments are couched in terms of directional trends rather than absolute values.

Future use of artificial propagation in the Columbia Basin will be a direct function of both the status of the natural populations and their habitats. For supplementation and recovery purposes, the productivity of the naturally spawning populations will be a key population parameter. Basically, if productivity is significantly >1, then populations can probably be recovered without the risks of artificial propagation. If the ratio is <1, and modeling shows that over time extinction will be imminent, then the benefits with artificial propagation should outweigh the risks. Artificial propagation risks may be ameliorated by development and implementation of conservation hatchery protocols which have the potential to improve fitness and survival of hatchery fish.

It is clear from this review that the Region needs to focus research to develop policies and procedures which properly integrate the roles of hatcheries for conservation and sustainability of salmonid populations. Information currently available is not adequate to assess properly the potential effects of hatchery operations on wild stocks. Among key questions to be answered by scientific research include:

- Is it possible to produce more adaptable wild-like juveniles from conservation hatcheries with the fitness necessary to aid rebuilding of ESA listed stocks?
- Is it possible to minimize the impacts on wild fish by releases from production hatcheries for sustainable fisheries?
- What are the relative probabilities of meeting the survival and recovery goals for salmon in the Columbia River Basin under different artificial propagation scenarios?

Finally, research data sets should be compiled in a manner to allow generalized correlation between indicators of natural population productivity and artificial propagation factors. Development of an overall complete understanding of the current and potential role(s) of hatcheries on the sustainability of natural stocks is a vitally important undertaking for rebuilding efforts for depleted stocks.

Table 10. Assessment of effects of hatchery steelhead smolt releases on the population abundance of wild steelhead.

	Effects on wild fish population abundance								
	Freshwater residence				Outmigration				
Hatchery influence	Egg-to-emergence	Age-0	Age-1	Age-2	Tributary	Mainstem	Estuary	Upstream migration	Spawning
A. Production strategy									
i) increasing release numbers		NEG/a	NEG/a	NEG/a					
ii) supplementation release strategy using out-of-basin hatchery stock		NEG	NEG	NEG					
iii) supplementation release strategy using local hatchery stock		NEG - POS	NEG - POS	NEG - POS					
iv) supplementation release strategy using locally adapted wild stock		POS	POS	POS					
v) implementation of conservation hatchery technology	UNK+	UNK+	UNK+	UNK+	POS	UNK+	UNK+	UNK+	UNK+
B. Competition									
i) exclusion from key habitat resources	N/A	N/A	N/A	AL	AL	AL	AL	AL	NEG - 0
ii) exclusion from key food resources	N/A	N/A	N/A	AL	AL	AL	AL	AL	AL
C. Predation									
i) direct predation	NLF	NLF	NLF	NLF	NLF	NLF	NLF	NLF	
ii) changes in predator/prey dynamics	AL	AL	AL	AL	AL	NLF	NLF	NLF	
D. Health status									
i) direct interactions	NLF	AL (neg)	NLF	NLF	AL (neg)	AL (neg)	NLF	NLF	AL (neg)
ii) contact through other vectors	NLF	AL (neg)	NLF	NLF	AL (neg)	AL (neg)	NLF	NLF	NLF
E. Migration									

NEG: literature indicates negative effect at selected life stage

POS: literature indicates positive effect at selected life stage

0: literature indicates no effect at selected life stage

UNK-: approach theoretical, relationship probably negative, studies have not been conducted

UNK+: approach theoretical, relationship probably positive, studies have not been conducted

AL: only ancillary literature available, no evidence of (positive - negative) directional effect at selected life stage

NLF: no literature found that addresses life stage impact

N/A: not applicable

a relationship could be positive at low population densities

b relationship could be positive at high population densities

Table 11. Assessment of effects of hatchery chinook salmon smolt releases on the population abundance and trends of wild chinook salmon.

	Effects on wild fish population abundance							
	Freshwater residence			Outmigration				
Hatchery influence	Egg-to-emergence	Age-0	Age-1	Tributary	Mainstem	Estuary	Upstream migration	Spawning
A. Production strategy								
i) increasing release numbers		NEG/a	NEG/a					
ii) supplementation release strategy using out-of-basin hatchery stock		NEG	NEG					
iii) supplementation release strategy using local hatchery stock		NEG - POS	NEG - POS					
iv) supplementation release strategy using locally adapted wild stock		POS	POS					
v) implementation of conservation hatchery technology	UNK+	UNK+	UNK+	POS	UNK+	UNK+	UNK+	UNK+
B. Competition								
i) exclusion from key habitat resources	N/A	N/A	N/A	AL	AL	0	0	NEG - 0
ii) exclusion from key food resources	N/A	N/A	N/A	AL	AL	NEG - 0	NEG - 0	N/A
C. Predation								
i) direct predation	0 - NEG	O - NEG	NLF	NLF	NLF	NLF	NLF	NLF
ii) changes in predator/prey dynamics	AL	AL	AL	AL	AL	NLF	NLF	NLF
D. Health status								
i) direct interactions	NLF	AL (Neg)	NLF	AL (Neg)	AL (Neg)	AL (Neg)	NLF	AL (Neg)
ii) contact through other vectors	NLF	AL (Neg)	NLF	AL (Neg)	AL (Neg)	AL (Neg)	NLF	NLF
E. Migration								

NEG: literature indicates negative effect at selected life stage
POS: literature indicates positive effect at selected life stage
0: literature indicates no effect at selected life stage
UNK-: approach theoretical, relationship probably negative, studies have not been conducted
UNK+: approach theoretical, relationship probably positive, studies have not been conducted
AL: only ancillary literature available, no evidence of (positive - negative) directional effect at selected life stage
NLF: no literature found that addresses life stage impact

N/A: not applicable
a relationship could be positive at low population densities
b relationship could be positive at high population densities

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APPENDIX

A. THE IMNAHA SPRING/SUMMER CHINOOK SUPPLEMENTATION PROJECT

Species:	Spring/summer chinook
Location:	Imnaha Basin, North Eastern Oregon
Starting Date:	1982 broodyear
Planned Duration:	Not known
Status:	On-going
Production Level:	25,000 to 445,000/year
Size:	25 g mean size for 1990-1994 (mean wt. range 21 - 41 g)

1. The Status of the Stock before Supplementation

The program was initiated under the Lower Snake River Compensation Plan as a mitigation program to provide surplus hatchery fish for harvest. The redd count in the Imnaha River Basin has shown a general decrease over the past 40 years (see Figure 1).

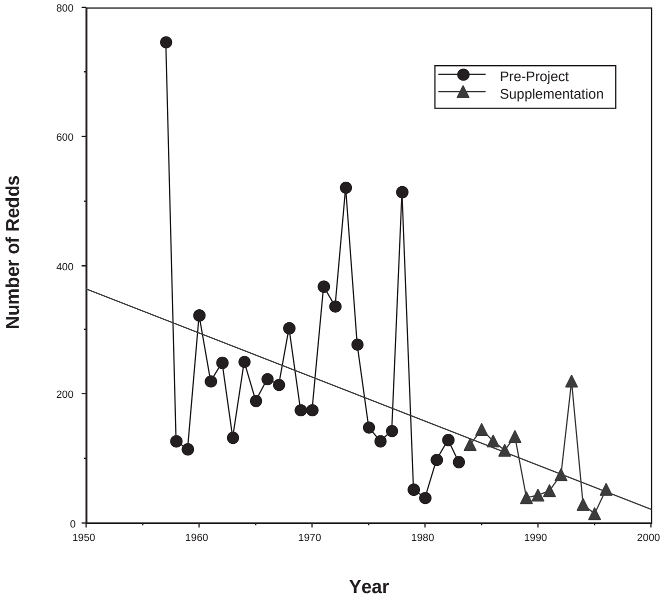

Figure 1. Redd counts, showing pre-project and supplement periods.

2. Monitoring and Evaluation

A monitoring and evaluation program was started in 1994. The objectives are to assess the effectiveness of the hatchery program in increasing adult production, adult progeny:parent ratios, and escapement to the Imnaha River; to estimate total annual adult production (catch and escapement), smolt-to-adult survival, and smolt migration success of hatchery fish; to monitor and compare life history characteristics of natural and hatchery fish; and to make recommendations for improving the success of achieving mitigation goals and management objectives (Carmichael and Messmer, 1995).

3. Results

The adult progeny:parent ratios (AD:P) of hatchery and wild fish (ODFW 1998) are detailed below:

Year	Wild Fish		Hatchery Fish	
	AD:P Ratio	Contribution[1]	AD:P Ratio	Contribution[1]
1982	1.05	105	8.82	882
1983	1.15	115	1.25	125
1984	0.26	26	3.08	308
1985	0.17	17	1.96	196
1986	0.41	41	1.52	152
1987	0.44	44	3.73	373
1988	0.72	72	12.6	1260
1989	0.55	55	3.81	381
1990	0.2	20	0.51	51
1991	0.2	20	1.09	109
1992	0.5	50	0.62	62
Average	0.51		3.54	
Total		565		3,899

[1] Adult contribution based on a hypothetical spawning of 50 pairs of salmon

4. Conclusions

Based on published AD:P ratios, it appears that this supplementation project may be increasing the number of returning adults. The AD:P ratio for the hatchery fish on the average, has been about 7 times larger than for the wild fish. (Note: there are significant differences in AD:P ratios listed in Carmichael and Messmer, 1995 and ODFW 1998. This is probably due to inclusion of jacks in the adult counts.)

Based on a hypothetical 50 pair program (see above table), the supplementation program would have contributed 3,899 adults over the 1982-1992 time period. If these hypothetical fish had been allowed to spawn in the wild, only 540 adults would have been produced. The overall population trend appears to still be downward (ODFW 1998).

B. THE BIG QUILCENE RIVER SUMMER CHUM SUPPLEMENTATION PROJECT

Species:	Chum salmon
Location:	Hood Canal, Washington
Starting Date:	1992
Planned Duration:	12 years
Status:	On-going
Production Level:	325,000 (mean) over last 7 years (range 24,784 to 612,598)
Size:	1.1 to 1.6 g

1. The Status of the Stock before Supplementation

In 1992 the stock was in critical condition (WDF et al. 1993). Escape had fallen to extremely low levels and habitat conditions had become very poor in the lower river where summer chum spawned. A supplementation project was begun in the Big Quilcene River and has for the most part been successful (SWG 1999).

2. Monitoring and Evaluation

Since the inception of the project there has been only limited marking of hatchery releases. Therefore differentiation between hatchery-origin and natural-origin fish on the spawning grounds has not been feasible. However, all brood year 1997 and 1998 hatchery releases were marked with adipose fin clips and it is expected such marking will continue the duration of the project (SWG 1999).

3. Results

Period	Status	Total Adult Escape over the Period		
		Big Quilcene (Control)	Dosewallip (Control)	Duckabush
1984 - 1994	Pre-supplementation	1,069	2,434	2,204
1995 - 1998	Supplementation	22,091	10,146	4,176
Increase over the Supplementation/ Pre-supplementation period (factor)		x21	x4.2	x1.9
Excess due to supplementation based average increase in controls		18,884	—	—

Assuming that the 18,884 “excess” fish are of hatchery origin and a mean release of 325,000, the smolt-to-adult return (SAR) of the hatchery fish would be 5.8%.

4. Conclusions

The Summer Chum Work Group considers this a successful supplementation project, even though it is currently impossible to distinguish returning wild and hatchery-origin fish. The escape to the Big Quilcene River has increased by a factor of x21 compared with the pre-supplementation levels. During this same period, the returns to the Dosewallip and Duckabush only increased by factors of x4.2 and x1.9, respectively. These increases in escapement could also be due to reduction in harvest rate, increases in marine survival, and improvements in freshwater habitat (Johnson et al. 1997).

C. THE MID-COLUMBIA FALL CHINOOK SUPPLEMENTATION PROJECT

Species:	Fall Chinook
Location:	Hanford Reach, Mid-Columbia
Starting Date:	1980
Planned Duration:	????
Status:	On-going
Production Level:	8.09 million fish for 1983-1992 (ranged from 5.4 to 11.8 million)
Size:	Release goal of 50/lb (9.1 g)

1. Status of the Stock before Supplementation

This program is operated as mitigation for fishery impacts caused by the Priest Rapids Projects (Priest Rapids and Wanapum dams). The current escapement appears to be relatively stable compared with the average historical run size. The increase in run size during the 1980s could be due to the hatchery program (Dauble and Watson 1997).

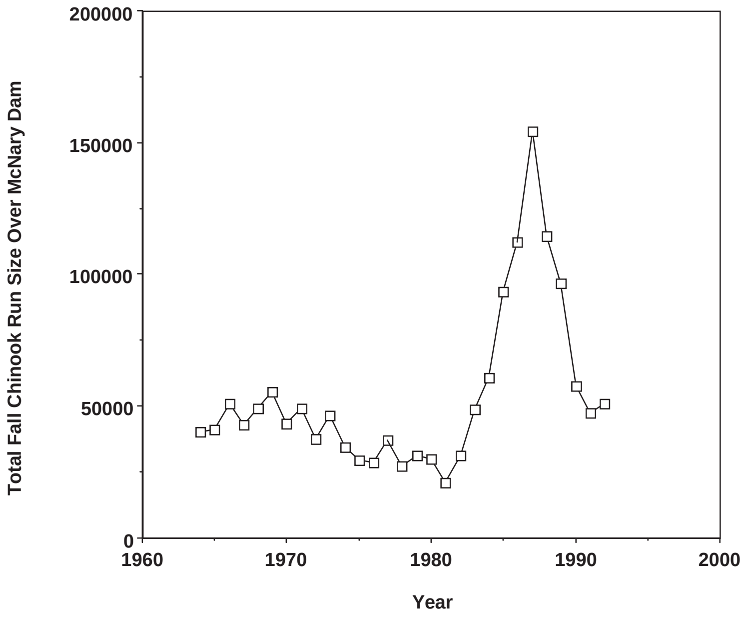

Figure 1. Estimated total run size of fall chinook to the Hanford Reach (Dauble and Watson 1997).

2. Monitoring and Evaluation

The portion of marked hatchery fish has ranged from 3-19% over the last 10 years.

3. Results

The adult progeny:parent ratios of hatchery and wild fish are detailed below:

Year	Wild Fish		Hatchery Fish	
	AD:P Ratio	Contribution[1]	AD:P Ratio	Contribution[1]
1980	1.76	880	8.37	4,185
1981	4.34	2,170	4.41	2,205
1982	4.54	2,270	3.83	1,915
1983	2.58	1,290	1.86	930
1984	2.82	1,410	1.59	795
1985	2.18	1,090	1.52	760
1986	0.50	250	1.54	770
1987	0.50	250	1.07	535
1988	0.41	205	1013	565
1989	0.61	305	1.65	825
1990	0.87	435	1.16	580
1991	0.92	460	1.42	710
Average	1.84		2.46	
Total		11,015		14,775

[1] Adult contribution based on a hypothetical spawning of 250 pairs of salmon

4. Conclusions

Over the period of 1980-1995, the percentage adult contribution from hatchery releases averaged 5% (PSMFS 1999). Therefore, this program is a minor contribution to the larger healthy wild stock.